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MICHEL E. HENDRICKX
LABORATORIO DE INVERTEBRADOS
BENTONICOS
ESTACION MAZATLAN ICML
UNAM
A POSTAL 811 MAZATLAN
82000 SINALOA, MEXICO

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DEDICATION

The Journal AMPHIPACIFICA is dedicated to the promotion of systematic biology and to the conservation of Earth's natural resources.

Cover design: Adapted from the title page of S. J. Holmes (1904).
"Amphipod Crustaceans of the Expedition."
Harriman Alaska Expedition, pages 233-244.

Editorial Commentary . .

With this issue Volume I of *Amphipacifica* and our first anniversary of desk-top publication of systematic studies on aquatic invertebrate animals is completed. The commentary of the readership, especially the guidance provided by editors and former editors of other research journals, has led to improvement in the format, and in mechanical aspects of publication. We are now using a Select 360 laser printer, with 600 d.p.i. capability, to enhance the quality of the print and line illustrations, especially those adapted from other publications. A recent switch to the Fleming Printing Company, West Victoria, B. C., now ensures total in-house control of printing and binding, at very competitive cost. The resulting savings are being passed on to the readers and contributors through continued low subscription rates and page charges. The increasing number of subscription renewals for volume II is an encouraging sign that the journal is favourably fulfilling its purpose.

Commentary on the journal has come from a wide spectrum of readers. Criticisms have been helpful, and tactfully phrased. General satisfaction has been expressed by Wim Vader, Tromsø, Norway; Mark Costello, Dublin, Ireland; Larry Hamblin, Romford, U. K.; John Holsinger, Norfolk, VA.; Patsy McLaughlin, Anacortes, WA; Ichiro Takeuchi, Japan; and delegates to the 8th Amphipod colloquium hosted by Krzysz Jazdzewski in Poland last September. The recent paper on amphipod phylogeny [Vol. I (3)] has been of special interest to several readers, including Hiroshi Morino, Ibaraki University, Pierre Noel, Université de Paris, and Fred Schram, University of Amsterdam. Fred has kindly drawn our attention to an alternative interpretation of the arrangement of pleopods of the male of *Metalingolfiella* that may prove to be a further autapomorphy within the primitive suborder Ingolfiellidea. Jim Lowry, Australian Museum, has also noted an apparent inconsistency in our figures of male and female specimens of *Rhepoxnius vigitegus* that, to clarify, may require re-examination of original material. Niel Bruce, University of Copenhagen Museum, Denmark, has drawn our attention to some editorial oversights, and problems of line quality and printing intensity in previous issues that we have attempted to adjust in this issue. Changes include a switch in position of the running head and pagination, more restrictive use of underlining, oversize letters, and boldface type, and reduced use of abbreviations in the references. We apologize for some "slippage" in our planned publication and mailing dates. Perfection is elusive, but with your help we may eventually approach that desirable level.

The Journal is continuing the policy of exchange advertising with other journals of systematic biology, and with societies and agencies concerned with conservation of natural resources. We welcome submissions of short studies, as well as medium to long papers, and review articles that involve some aspect of aquatic biology and/or environmental concern. Although the journal focuses on aquatic

invertebrates of the North Pacific, analytical accounts of other biotas (including vertebrates and fossil animals), of other biomes (including terrestrial), and other world regions are invited.

The principal topic of the two major papers of this issue is the biosystematics of eusiroidean amphipods of the North American Pacific region. A short paper on Cambrian marine arthropods, intended for this issue, regrettably could not be refereed or edited in time for publication and will appear in volume IV, hopefully the better for the delay.

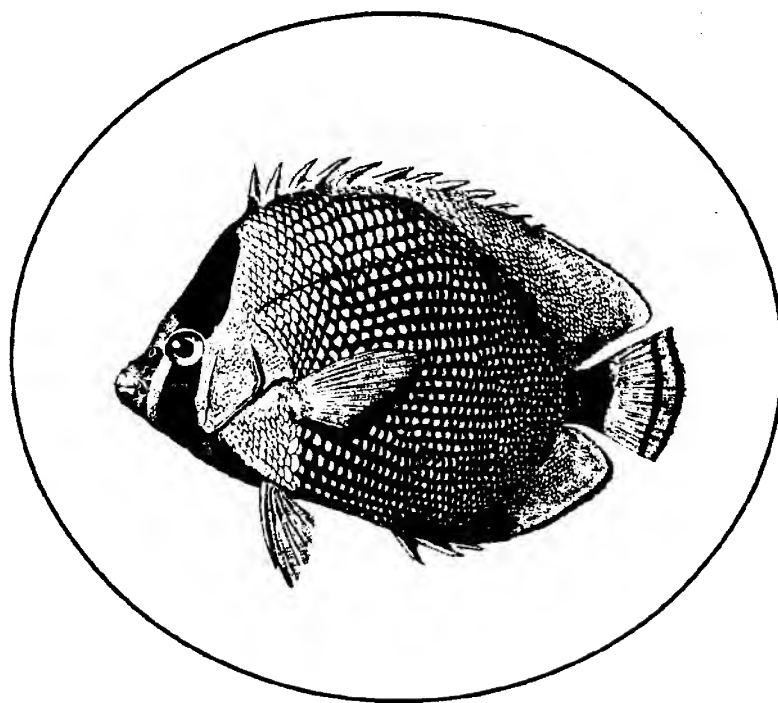
The first paper treats family Eusiridae, members of which are relatively large, epibenthic and pelagic raptorial amphipods, the so-called "dragonflies of the deep", that prey mainly on smaller crustaceans in the water column, from sublittoral to abyssal depths. North Pacific coastal waters yielded several new species, some of a type found nowhere else. The region also encompasses a high percentage of the known world genera and species of Eusiridae, qualifying it as a major centre of origin and evolution of the family as a whole. Perhaps not surprisingly the authors found that, in relation to the eusirid fauna of the geologically younger and subducting North American Pacific coast, the eusirid fauna of the older western North Pacific region is taxonomically more diverse and contains a higher percentage of relatively primitive genera and species.

In the second paper, Craig Staude newly describes the morphology, ecology, and reproductive behaviour of members of the speciose but relatively primitive pontogeneiid genus *Paramoera*. He discovered a rich complex of nine species, six new to science, that live mainly along stony and gravely beaches, from southeastern Alaska to central California. Although the animals are strong swimmers, they feed mainly on algal/organic detritus on, or interstitially within, the substratum. Males have developed, variously, specialized modifications of the gnathopods and pleopods, associated with the mating process, in their wave exposed, physically rigorous habitats. In placing the North American Pacific fauna taxonomically and phylogenetically within the much larger world (especially subantarctic) complex of species, the author created three new subgenera of *Paramoera* to encompass species of the entire North Pacific region, including Hawaii.

The bathymetrical range of the aquatic animals encompassed by current studies extends from eulittoral and subtidal habitats to the ocean abyss, a range that we hope will reflect the breadth of research submissions in future numbers of *Amphipacifica*. In coming issues of Volume II, readers may look to further comprehensive accounts of North Pacific crustaceans, particularly of the large amphipod families Oedicerotidae, Melitidae, Calliopidae, Hyalidae, and further Pleustidae. We anticipate shorter accounts of the sand-burrowing Haustoriidae, the kelp gall-forming Najnidae, and the tube-dwelling Corophiidae. Some species of the latter family appear to have been synanthropically introduced into North American Pacific waters, and may be in the process of ecological replacement of regional endemics.

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THE AMPHIPOD SUPERFAMILY EUSIROIDEA IN THE NORTH AMERICAN PACIFIC REGION. I. FAMILY EUSIRIDAE: SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

by E. L. Bousfield¹ and E. A. Hendrycks²

ABSTRACT

The gammaridean amphipod family Eusiridae encompasses a group of marine epibenthic and pelagic carnivorous amphipods that prey mainly on other small crustaceans. The family is represented in the northeastern Pacific coastal marine region, from Alaska to central California, by fourteen species of the genus *Rhachotropis*, of which the following are fully described and figured here: *R. aculeata* (Lepechin, 1780), *R. oculata* (Hansen, 1882), *R. boreopacifica*, new species, *R. conlanae*, new species, *R. minuta*, new species, *R. calceolata*, new species, *R. americana*, new species, *R. distincta* (Holmes, 1908), and *R. natator* (Holmes, 1908). Taxonomic notes and commentary are provided on other regional sublittoral (eyed) species: *R. inflata* Sars, 1895, *R. helleri* (Boeck, 1871), and *R. macropus* Sars, 1895. *Rhachotropis clemens* Barnard, 1971 (eyed variant) from the coasts of Oregon to British Columbia, is redescribed as *R. barnardi*, new species. Based mainly on the literature, the study briefly treats sublittoral, bathyal, and abyssal species *R. luculenta* Barnard, 1969c, *R. ludificor* Barnard, 1967, *R. clemens* Barnard, 1967, *R. multesimus*, Barnard, 1967, and *R. gubilata* Barnard, 1964, mainly from other N. American Pacific regions, and *R. grimaldi* (Gurjanova form) from the western Pacific. *Eusirus longipes* (Boeck), figured by Hirayama from Japan, is redescribed here as *E. hirayamae*, new species. Also described and illustrated from the study region are *Eusirus cuspidatus* Kroyer, 1845, and *Eusirus columbianus*, new species, *Eusirella multicalceola* (Thorsteinson, 1941), and *Cleonardo moirae*, new species. Of the thirteen genera here comprising family Eusiridae, *Eusiroides* was found to be morphologically the most primitive, and *Eusirella* and *Rhachotropis* the most advanced genera. Within genus *Rhachotropis*, the holarctic benthic *R. aculeata* proved to be the most primitive, and the bathypelagic *R. natator* and *R. distincta* the most advanced species.

Biogeographically, the North Pacific region may be considered a major centre of eusirid evolution since it contains representatives of 10 of the 13 world genera, and its 35 species represent about 30% of the known world fauna. The eusirid fauna of the western (Asiatic) North Pacific appears more diverse at genus level and contains more primitive taxa. By contrast, the advanced genus *Rhachotropis* contains half the total North Pacific eusirid fauna and two-thirds of that fauna, including the most primitive and most advanced members, are recorded from the eastern (American) North Pacific region, here considered to be a major centre of origin and evolution of the group.

INTRODUCTION

Members of the amphipod family Eusiridae are medium to large epibenthic and pelagic marine carnivores that prey mainly on various benthic invertebrates or small fast moving crustaceans in the water column. The abdominal segments, pleopods, and tail fan of eusirids are typically large and powerfully developed, and function in rapid propulsion and change of direction. Eusirid sensory mechanisms include, typically, very large multi-faceted eyes, and antennal calceoli of a complex type that are presumed to detect acoustical or mechanical vibrations from prey organisms. Morphological adaptations for this life style consist of large raptorial gnathopods and maxillipeds by means of which prey organisms are rapidly captured, killed, and thrust towards the chewing mouthparts (Klages & Gutt, 1990). Deep-water eusirids employ their slender, long-dactylate pereopods for standing on soft bottom sediments while awaiting benthic prey, or possibly as a raptorial "basket" in which prey organisms are entrapped when feeding pelagically (see also Enequist, 1950).

Eusirids tend to occur in deep coastal fiords and offshore waters, presumably where diurnal vertical migrations can be

effected in concert with movements of their prey. Many eusirid species are entirely abyssal, not captured in the euphotic zone at any time. The Eusiridae is one of several natantian gammaridean families (see Bousfield & Shih, 1994), including those among superfamilies Pardaliscoidea, Lysianassoidea, Stegocephaloidea, and Melpheippoidea, and among reptantian family Melitidae, whose members are specialized as pelagic predators. In size, functional morphology, and life style, members of these groups appear similar to hyperiid amphipods; all may be viewed, by 3-dimensional predatory analogy, as "dragonflies of the deepes". However, eusirid species themselves serve as prey organisms of regional food fishes, either directly or indirectly, and thus are important in marine food energy cycles.

The history of development of systematic knowledge of eusirid amphipods on the North American Pacific coast is relatively limited. Nineteenth century regional records are not included in Stebbing (1906). The first confirmed records were those of *Gracilipes natator* and *G. distincta* by Holmes (1908), from off the coast of California. Thorsteinson (1941) included those species and her new species *G. multicalceola* from off the coast of Washington State. Shoemaker (1925) added *R. natator* from the Gulf of California, and *R. acule-*

¹ Researcher Emeritus, Canadian Museum of Nature, Ottawa, Canada K1P 6P4

² Canadian Museum of Nature, Ottawa, Canada K1P 6P4

eata and *Eusirus cuspidatus* from the Pt. Barrow region of Alaska. J. L. Barnard published a number of important new records, commencing with redescription of *R. natator* from California (1954) followed by an extensive series on bathyal species (1957, 1964, 1967, 1971, etc.), and culminated in his most useful world compendium (with Gordan Karaman, 1991). A few records from the northwestern Pacific region had been summarized by Shoemaker (1955), Austin (1985), and Staude (1987).

The rich Asiatic Pacific eusirid fauna has been described and catalogued almost entirely within the last 50 years, mainly by Gurjanova (1951), Birstein & Vinogradov (1955, 1958, 1960), Hirayama (1985), and Ishimaru (1994).

The purpose of this investigation is to develop new taxonomic, ecological, and biogeographical information on the gammaridean amphipod family Eusiridae in the northeastern Pacific region, based mainly on recently collected material. This fauna, previously little studied, provides a connecting link between the relatively well known eusirid assemblages southward along the N. American Pacific coast, and those of the Asiatic Pacific region. The integrated results thereby facilitate analysis of the entire North Pacific fauna in the context of family Eusiridae on a world-wide basis.

ACKNOWLEDGEMENTS

Of the 18 species of family Eusiridae recorded authentically from the study region (Table III, zones 3-7), 8 species (5 new to science) were obtained from ~60 collections made by NMNS (CMN) expeditions to the study region during the period 1955-1980 (types deposited in the CMN), and an oceanographic survey in 1991. The station data and detailed acknowledgement of field assistance are provided in the published station lists of the senior author and collaborators (Bousfield, 1958, 1959, 1968; Bousfield & McAllister, 1963; Bousfield & Jarrett, 1981). Several lots of material of the Institute of Ocean Sciences (IOS), Sidney, B. C. (see Thomson et al, 1992), containing 3 regional oceanic species (1 new to science), were kindly made available to us by Moira Galbraith, Sy-Tech Research Ltd., Sidney, B. C. The authors are pleased to name (from this material) *Cleonardo moirae*, new species, in her honour (p. 15). Two large arctic and subarctic species were found in benthic material from the Bering Sea region kindly provided by Dr. Peter Slattery, Moss Landing, California. A single lot of specimens collected by Kathleen E. Conlan (CMN under grant DPP-2619394 to Dr. John Oliver, Moss Landing, CA, contained a distinctive new species of *Rhachotropis* (see p. 38). Collection abbreviations and plate legends are tabled on p. 56.

We are grateful for helpful commentary in the preparation of this report provided over the years by research colleagues C-t. Shih and K. E. Conlan (CMN), Patrick Shaw, Vancouver, B. C., C.P. Staude, Friday Harbor, WA, and Wim Vader, Tromsø, Norway. Susan Laurie-Bourque, Hull, Que., most capably assisted with the line illustrations. Translation of Russian text was provided by Marjorie Bousfield, Montreal, Quebec.

SYSTEMATICS

Superfamily Eusiroidea

Eusiroidea Bousfield 1979: 255.—Bousfield, 1982: 263. — Schram, 1986: 178.—Staude 1987: 377.

Eusiridae: Barnard, 1969a: 213 (part).—Barnard & Karaman, 1991: 284 (part).—Ishimaru, 1994: 44.

Type family. Eusiridae Stebbing, 1888.

Families: Pontogeneiidae Stebbing, 1906 - type genus *Pontogeneia* Boeck, 1871; Bateidae Stebbing, 1906 - type genus *Batea* Muller, 1865; Calliopiidae Kroyer, 1845 - type genus *Calliopius* Liljeborg, 1865; Eusiridae Stebbing, 1888 - type genus *Eusirus* Kroyer, 1845; Gammarellidae Bousfield, 1977 - type genus *Gammarellus* Herbst, 1793; Amathillopsidae Heller, 1875 - type genus *Amathillopsis* Heller, 1875; Gammaracanthidae Bousfield, 1989 - type genus *Gammaracanthus* Bate, 1862; Paramphithoidae Stebbing, 1906 - type genus *Paramphithoe* Bruzelius, 1835.

Note: Southern continental freshwater eusiroidean genera, presently included in family Calliopiidae (e.g. *Paraleptamphopus* Stebbing, 1899; *Falklandella* Schellenberg, 1931; *Praefalklandella* Stock & Platvoet, 1993) may require separate family recognition.

Diagnosis (modified from Bousfield, 1982): Body medium to large, often dorsally, dorso-laterally, occasionally laterally processiferous. Rostrum often strong. Eyes usually large (often lacking in abyssal and hypogean forms). Antennae medium, not greatly elongate. Calceoli variously present, on distal peduncular and flagellar segments of both antennae, often in both sexes, or lacking; calceoli complex, often of sexual and asexual types, with receptacle, bulla, and modified distal elements. Antenna 1, callynophore weak or lacking; accessory flagellum short, vestigial or lacking. Antenna 2 (male): peduncular segments 4 & 5 often with brush setae; flagellum not greatly elongate.

Mouthparts basic, typically modified for carnivory. Upper lip, lower margin rounded. Lower lip, inner lobes lacking or weakly developed. Mandible, molar strong, triturative, or reduced; left lacinia 5-8+ dentate, right lacinia flabellate or trifold; spine row short; palp strong, segment 3 often falcate or elongate. Maxilla 1, outer plate with 11 (occ. fewer) apical spines, inner plate variously setose, palp 2-segmented. Maxilla 2, plates normal, inner plate, facial setae strong, less often few or lacking. Maxilliped normal, plates and palp strong, often raptorial.

Coxal plates 1-4 usually medium to large, occ. small, increasing in size posteriorly, usually lacking lower hind cusps. Gnathopods typically subsimilar in form and size, variously subchelate, not (or weakly) sexually dimorphic; carpus often shortened or modified, palms and dactyls smooth.

Peraeopods 3 and 4 regular, subsimilar, dactyls often strong or elongate. Peraeopods 5-7 basically homopodous or slightly heteropodous; 7 usually longest; coxae 5-7 postero-lobate; segments 4-6 spinose, often elongate in abyssal

KEY TO FAMILIES OF SUPERFAMILY EUSIROIDEA

1. Telson distinctly bilobate or deeply cleft in most members 2.
—Telson plate-like or weakly notched apically 5.
2. Gnathopods large, strongly subchelate, often "eusiroidean" in form; peraeopods 5-7 generally elongate, slender; animals often large (10-40+ mm) 3.
—Gnathopods weakly or moderately subchelate (esp. in female); peraeopods 5-7 regular, stout, not elongate; animals small to medium (< 10 mm) 4.
3. Antenna usually calceolate (often in both sexes); accessory flagellum small, 1-2 segmented; telson large, cleft or notched distally; peraeopod 7 longer than 6 Eusiridae (p. 6)
—Antennae lacking calceoli; accessory flagellum prominent 3-7+ segments; telson very short, fully bilobate; peraeopod 7 not longer than 6 Gammaracanthidae
4. Gnathopods 1 and 2 normally subsimilar, subequal; peraeopods 5-7 generally homopodous in size and form Pontogeneiidae
—Gnathopod 1 (and coxa) vestigial; peraeopods 5-7 similar in size but distinctly heteropodous in form Bateidae
5. Coxae 1-4 acute or strongly toothed below; peraeon strongly dorsally carinate; peraeopod 7 not larger (longer) than peraeopod 6 6.
—Coxae 1-4 rounded or truncate below; peraeon smooth dorsally (except Gammarellidae); peraeopod 7 larger than peraeopod 6 7.
6. Body variously carinated or processiferous dorsolaterally and often laterally; gnathopods with weak carpal lobes; antenna 1, peduncular segments 1 & 2 each shorter than head Paramphithoidae
—Body mid-dorsally toothed only; carpal lobes of gnathopods deep; antenna 1, peduncular segments 1 and 2 each longer than head Amathillopsidae
7. Peraeon not (rarely) carinate; accessory flagellum minute (rarely 2-4 segmented); calceoli (when present) of a simple, single pontogeneiid type 8.
—Peraeon weakly mid-dorsally carinate; accessory flagellum distinct (4-6+ segments); calceoli of two types, complex, proximal and distal elements separate Gammarellidae
8. Pleon often dorsally carinate or toothed; gnathopods closely subequal in size (both sexes); coxal gills pleated, especially in male; sternal gills lacking; marine Calliopiidae
—Pleon dorsally smooth; gnathopod 1 distinctly the larger; coxal gills simple; sternal gills often present; continental fresh waters of Australia, New Zealand, & Falkland Islands (potential new family)

forms; segment 4 little produced posterodistally, not strongly overhanging segment 5.

Pleon typically large, often dorsally carinate; pleopods powerful, sexually dimorphic in size, occasionally in form; pleon plates normal or toothed behind. Uropods 1 & 2 lanceolate, sublinear, serially spinose, apically spinose in littoral and freshwater groups. Uropod 3, rami typically lanceolate, margins serially spinose and/or setose; outer ramus 1-segmented, often reduced, spinose in freshwater groups. Telson large, bilobate, or lobes variously fused to entire plate, lacking ventral keel (e.g. of Pleustidae).

Coxal gills plate-like, often pleated (or double), especially in male, on peraeopods 2-7 (rarely lacking on 7),

secondarily simple (pleats lost); sternal gills often present in fresh-water members. Brood plates broad, marginal setae simple, numerous. Males typically smaller than females; usually mating freely in the water column.

Distributional Ecology. Essentially bipolar; dominant in coldwater marine regions, coastal and neritic to abyssal, occasionally estuarine and freshwater along continental coasts of Australia, New Zealand, the Falkland Islands, Japan, and Indo-Pacific Islands, but apparently not South America. A relatively ancient group, retaining many presumed ancestral gammaridean character states.

Taxonomic commentary: Following Bousfield & Shih (1994), the following families have been transferred to superfamily Leucothoidea: Acanthonotozomatidae Stebbing, 1906 - type genus *Acanthonotozoma* Boeck, 1875; Laphystiopsidae Stebbing, 1906 - type genus *Laphystiopsis* G. O. Sars, 1895; and Lafystiidae G. O. Sars, 1895 - type genus *Lafystius* Kroyer, 1842.

Eusiridae Stebbing

Eusiridae Stebbing, 1888: 953.—Stebbing, 1906: 327 (except *Rozinante*).—Gurjanova, 1951: 698 (except *Rozinante*).—Bousfield, 1973: 77.—Lincoln, 1979: 402.—Ledoyer, 1982: 233.—Bousfield, 1982a: 264.—Ishimaru, 1994: 44.—Bousfield & Shih, 1994: 128.
Eusiridae (partim) J. L. Barnard, 1969a: 213.—Barnard & Karaman, 1991: 284.

Type Genus. *Eusirus* Kroyer, 1845

Genera: *Eusiroides* Stebbing, 1888 (15 spp., mainly tropical, littoral and sublittoral); *Eusirella* Chevreux, 1908 (5 spp., mainly North Pacific, abyssal); *Eusirogenes* Stebbing, 1904 (5 spp., mainly northern oceans); *Eusiropsis* Stebbing 1897 (2 spp., North Pacific, Antarctic, abyssal); *Eusirus* Kroyer, 1845 (24 spp., cosmopolitan, littoral to abyssal); *Pareusirogenes* Birstein & Vinogradov, 1955 (1 species, Okhotsk Sea, bathyal); *Meteusiroides* Pirlot, 1934 (Indian ocean, mesopelagic); *Harclado* J. L. Barnard, 1964c (tropical Atlantic, Indian, & Pacific oceans, mesopelagic); *Cleonardo* Stebbing, 1888; (9 spp., 4 in North Pacific, bathy-pelagic); *Cleonardopsis* K. H. Barnard, 1916 (1 species, off S. Africa, bathypelagic); *Stenopleura* Stebbing 1888 (tropical Atlantic, North Pacific, mesopelagic); *Stenopleuroides* Birstein & Vinogradov 1964 (Indian Ocean, mesopelagic); *Rhachotropis* S. I. Smith 1883 (~50 species, mostly in northern oceans; some sublittoral, but mostly bathyal, and bathy-pelagic).

Diagnosis: Body medium small to medium large; processiferous dorsally and dorso-laterally on pleon, often on posterior segments of the peraeon, and on urosome 1. Peraeonal segments relatively short and compacted; pleonal segments large. Rostrum short to medium strong. Anterior head lobe broad, rounded or acutely produced (*Rhachotropis*). Eyes (when present) large, reniform to rhomboidal. Antennae 1 & 2 well developed, usually calceolate, usually on peduncle & flagellum, in both sexes. Antenna 1 usually shorter than 2; peduncular segment 3 short; flagellum of antenna 1 may be elongate in male; accessory flagellum small (1-2 segmented), scale-like, or lacking.

Mouthparts modified for carnivory. Upper lip rounded below, epistome not produced. Lower lip, inner lobes weakly developed. Mandible: molar conical, triturate; with short flagellum; blade row short; left lacinia 5-8+ dentate, right lacinia bifid; incisor strong, dentate; palp

elongate, slender, segment 3 often elongate. Maxilla 1, inner plate with 4-0 setae; outer plate with 11-9 apical spines; palp 2-segmented, proximal segment relatively long. Maxilla 2, inner plate broader than outer, facial setae reduced to single marginal seta or lacking. Maxilliped, palp strong, 4-segmented; outer plate slightly reduced; inner plate with 3+ apical spines.

Coxae 1-4 large to medium small, 4th largest, excavate behind; coxa 1 often produced anteriorly. Gnathopods 1 & 2 usually strongly subchelate, raptorial, subsimilar, 2 usually the larger; carpus usually shortened, hind lobe deep (rhachotropid form), or slender, elongate, lobe short, acute (eusirid form); basis often lined posteriorly with short spines.

Peraeopods 3 & 4 slender, bases extending beyond coxae; segment 4 usually longer than 5; dactyls strong. Peraeopods 5-7 slender, trending to dissimilarity in size and form, and elongation of distal segments and dactyls in abyssal forms.

Pleon plates regular, hind margin often serrate, hind corners not produced. Pleopods powerful, rami not sexually dimorphic. Uropods 1 & 2, rami lanceolate, serially spinose, usually lacking apical spines (except in *Eusiroides*), outer ramus distinctly the shorter. Uropod 3, rami subequal, margins serially spinose and/or weakly plumose setose. Telson usually elongate, lobes deeply and narrowly separated distally, apices acute; rarely short, and/or nearly totally fused at apex.

Coxal gills large, may be weakly pleated in male.

Taxonomic commentary. Component genera may be clustered into four main groups about the 65-70% similarity level (see Table I and Fig. 33) viz, the primitive littoral and sublittoral genus *Eusiroides*; an advanced littoral-pelagic abyssal *Rhachotropis-Eusirella* group, and two intermediate groups consisting of a relatively primitive *Cleonardo-Harclado-Stenopleura* complex, and a slightly more advanced sublittoral, bathyal, and bathypelagic *Eusirus-Eusirogenes* group. Within groups, component genera are separated at about the 80-85% level, not very far apart, and sharing some characters that may be convergent, but the bulk appear to be phyletic. Although the free-swimming deep-water genera entrain primitive reproductive and urosomal features, the mouthparts and peraeopods are advanced, suggesting specialization for capturing scarce, fast-moving prey organisms in the open ocean. The heavily plumose-setose peraeopods and uropod 3 of *Eusiropsis riisei*, and setose peraeopods 3 and 4 of *Eusirella multicalceola* may be flotation devices that assist in conserving energy in a food-deficient environment.

Birstein & Vinogradov (1958) have included *Stenopleura* in family Calliopiidae on the basis of its fused telson lobes. In all other diagnostic features above, however, *Stenopleura* conforms most closely with family Eusiridae. *Rozinante* was earlier removed to Calliopiidae (Bousfield, 1982). De Broyer and Jazdzewski (1993) have included *Atyloella*, Schellenberg, 1929, *Djerboa* Chevreux, 1906, *Liovillea*

KEY TO NORTH PACIFIC GENERA OF EUSIRIDAE

1. Gnathopods 1 and 2 distinctly eusiroidean in form (carpus slender, elongate, with narrow hind lobe, attached antero-distally to propod (Fig. 1) 2.
—Gnathopods 1 and 2, carpus short and deep or, if elongate, hind lobe broad, attached proximally to propod (Fig. 6) 5.
2. Gnathopod 1, propod distinctly larger than in gnathopod 2 *Eusirogenes* (p.21)
—Gnathopod 1, propod smaller than in gnathopod 2 3.
3. Coxal plates 1-4 deep, smooth below; accessory flagellum 1-segmented. *Eusirus* (p. 8)
—Coxae shallow, length > depth; accessory flagellum scale-like or lacking 4.
4. Peraeopods 3-7 distally plumose-setose; pleon dorsally smooth; mandibular molar reduced.
..... *Eusiroopsis* (p. 21)
—Peraeopods 3-7 normally dactylate and spinose distally; pleon weakly toothed mid-dorsally; molar normal, triturative surface large *Pareusirogenes* (p. 21)
5. Peraeopods 3 and 4, segment 4 not longer (often distinctly shorter) than 5; coxa 1 usually produced anteriorly; anterior head lobe acute; pleon 1-3 usually dorsally toothed, mucronate . . . *Rhachotropis* (p. 22)
—Peraeopods 3 and 4, segment 5 > segment 4; coxa 1 little produced or rounded anteriorly; anterior head lobe normal, shallow; pleon dorsal teeth usually lacking 6.
6. Coxa 1 expanding distally; peraeopods 5-7 short, segments stout; uropods 1 and 2, rami linear, apically spinose; uropod 3, ramal margins setose. *Eusiroides* (p. 8)
—Coxae 1 parallel-sided; peraeopods 5-7 slender, often elongate; uropods 1 and 2, rami lanceolate, with single spine or none at apex; uropod 3, ramal margins spinose or smooth, not setose. 7.
7. Gnathopods 1 and 2, propod slender, carpus elongate; maxilla 1, palp short, segments 1 & 2 subequal; outer plate with 9 apical spines *Eusirella* (p. 17)
—Gnathopods 1 and 2, propod stout, deep, carpus short, deep; maxilla 1, palp normal, distal segment much the longer; outer plate with 11 apical spines 8.
8. Pigmented eyes lacking; coxae 1-4 normal; accessory flagellum 1-segmented *Cleonardo* (p. 14)
—Eyes pigmented; coxae 1-4 small, shallow; accessory flagellum lacking 9.
9. Telson elongate, deeply cleft; gnathopod propods, palm nearly horizontal *Haracleo* (p.21)
—Telson short, apex shallowly notched or entire; gnathopod palms usually oblique . . *Stenopleura* (p. 21)

Chevreux, 1911, and *Schraderia* Pfeffer, 1888 in family Eusiridae. These 4 genera are excluded here because of their weak gnathopods, facial row of setae on the inner plate of maxilla 2, and pontogeneioid telsons, among other features.

Within the North Pacific region, the genera *Eusirus*, *Eusiroides*, *Eusirella*, *Cleonardo*, and *Rhachotropis* are amphi-North Pacific. However, within the North Pacific broadly, the genera *Haracleo*, *Stenopleura*, *Pareusirogenes*, *Eusiroopsis*, and *Eusirogenes*, have been recorded only from western regional waters and only on the basis of one or two species each, all from bathyal and abyssal depths (Ishimaru, 1994; Birstein and Vinogradov, 1955, 1958, 1960). The monotypic genera *Cleonardopsis* and *Stenopleuroides* are known only from abyssal waters of the North and South Atlantic, and the Indian oceans respectively (Barnard & Karaman, 1991).

Barnard and Karaman (1991) have effectively elevated the family Eusiridae to superfamily level by submerging

within it virtually all families of the present superfamily Eusiroidea. However, the families of Eusiroidea are fairly readily separable on morphological, biogeographical, and to some extent ecological and behavioural grounds. For example, families Eusiridae and Pontogeneiidae, maintained separately by most authors (e.g. Ledoyer, 1982), have been fused as one family (e.g. Barnard, 1969a) on the basis of a superficially similar "deeply cleft telson". These two groups actually differ clearly in all categories. With few exceptions, members of family Eusiridae have carnivorous mouthparts, and elongate, raptorial "lentic water" appendages; the species are fully marine sublittoral, bathyal and bathypelagic, and almost exclusively predaceous in feeding behaviour. By contrast, the Pontogeneiidae have generalist feeding mouthparts and short sturdy "lotic water" appendages; the species are essentially marine littoral, but occur often in brackish and fresh water and are almost exclusively omnivorous or detritivorous, seldom carnivorous, in feeding style.

Eusiroides Stebbing

Eusiroides Stebbing, 1888: 969.—Barnard & Karaman, 1991: 319.

Type species. *Atylus monoculoides* Haswell, 1879.

Component North Pacific species: *Eusiroides japonica* Hirayama, 1985: 36, figs. 149-154; *Eusiroides diplonyx* Barnard, 1970a: (Hawaiian Islands); *Eusiroides monoculoides* (Haswell) in J. L. Barnard, 1964, and Barnard (1969b) (So. California).

Taxonomic and biogeographical commentary. The genus *Eusiroides* has been fully rediagnosed by Barnard & Karaman (1991). It entrains most of the plesiomorphic character states found in eusiroidean genera, and its unique character states (e.g. linear, apically spinose uropod rami, spinose propodal palmar margins of the gnathopods, and stout homopodous peraeopods) are mainly plesiomorphic and typical of littoral marine pontogeneiids with which family group it appears to form a connecting link. However, *Eusiroides* does exhibit combinations of character states such as reniform pigmented eyes, deep coxal plates (coxa 1 broadly expanded distally), broadly homopodous peraeopods 5-7, setose rami of uropod 3, and pencil-like, 1-segmented accessory flagellum that, in combination, relate it to the more advanced genus *Eusirus* whose members are mainly epibenthic and sublittoral.

The genus *Eusiroides* contains about 15 species that are mainly warm-temperate and tropical, in Atlantic, Indian, and austral Pacific coastal marine regions. The type species, *E. monoculoides* (Haswell, 1879) has been identified from depths of 0-20 m at Corona del Mar, S. California, by J. L. Barnard (1964; 1969b), but this identification has not been confirmed subsequently. The species is unrecorded on the N. American Pacific coast north of that point. It is distinguished from the Hawaiian and western Pacific species by characters of the text.

Eusirus Kroyer

Eusirus Kroyer, 1845: 511.—Stebbing, 1906: 338.—Gurjanova, 1951: 698.—Birstein & Vinogradov, 1960: 220.—Barnard, 1969a: 226.—Ledoyer, 1982: 235.—Barnard & Karaman, 1991: 320.

Type species. *Eusirus cuspidatus* Kroyer, 1845

Component North Pacific species: *Eusirus cuspidatus* Kroyer, 1845; *E. hirayamae*, new species; *E. columbianus*, new species; *E. fragilis* Birstein & Vinogradov, 1960; *E. bathybius* Schellenberg, 1955 (Birstein & Vinogradov, 1960) (see also Fig. 40, p. 59, but not treated in text).

Diagnosis: Pleon, occasionally posterior peraeonal segments, weakly toothed and/or ridged postero-dorsally; urosome smooth above. Rostrum short. Anterior head lobe broad, oblique, weakly incised. Pigmented eyes medium,

reniform, or lacking. Antennae well developed, peduncles strong; distal peduncular segments and flagella calceolate in most species, in both sexes. Calceoli complex, with separate cup-like proximal and rod-like distal elements. Antenna 1 longer than antenna 2; peduncles 1 and 2 often cusped, or processiferous distally; peduncle 3 short; accessory flagellum distinct, linear, 1-2 segmented.

Mouthparts modified for carnivory. Upper lip, apex rounded. Lower lip, inner lobes weakly developed. Mandible: molar columnar and triturate; left lacinia 6-8 dentate, right lacinia bifid; palp slender, segment 3 usually longer than 2. Maxilla 1, inner plate with 1 apical seta, outer plate with 11 apical spines (10 pectinate); palp slender, outer segment longest. Maxilla 2, inner plate lacking facial setae, broader than outer. Maxilliped, palp large, raptorial; inner plate short, apex with 2-3 spines; outer plate large.

Coxae 1-3 medium, deeper than wide; coxa 1 broadened distally, hind corner cusped; coxa 4 excavate behind. Gnathopods strongly subchelate, "eusiroidean" in form (carpus slender, elongate, posterior lobe small, narrow; propod short, very deep), subequal in size and form, palmar margins lacking stout spines; merus and ischium small.

Peraeopods 3 and 4 slender, elongate; segment 4 > segment 5; dactyls short to medium. Peraeopods 5-7 slender, homopodous, increasing posteriorly; bases broad, hind margins often serrate, narrowing distally, lobate below.

Pleon plates 2 and 3 deep, broad, hind margin of 3 rounded, usually serrate. Uropods 1 and 2 slender, rami narrowly lanceolate, serially spinose, apices lacking spines; uropod 1, peduncle usually armed with stout antero-distal spine. Uropod 3, rami lanceolate, subequal, margins spinose, occasionally weakly plumose-setose. Telson large, elongate, narrowing distally, apex narrowly and deeply cleft.

Coxal gills large, weakly pleated. Brood plates broad, margins simple-setose.

Taxonomic and distributional commentary. Of the 24 described species and forms of the genus *Eusirus*, two-thirds occur mainly in sublittoral coastal, or bathyal and abyssal offshore waters of the North Atlantic, Arctic, and Antarctic regions, and the remainder in the Indian and North Pacific oceans. In more detailed breakdown, 14 of the species have pigmented eyes and are sublittoral in depths of less than 500 m. All nine species that have been recorded from Arctic and Antarctic waters are essentially sublittoral, with pigmented eyes. Of the 7 Atlantic species, three are sublittoral, with pigmented eyes, whereas of the 8 species recorded from the Indian and North Pacific oceans, only two are sublittoral and fully eyed, and both occur in the North Pacific (p. 10). These limited data would suggest that the genus *Eusirus* is essentially bipolar, with relatively few members penetrating towards the tropics at bathyal and abyssal depths. As we shall see below (p. 22), this pattern contrasts with that of the relatively advanced genus *Rhachotropis* in which 2/3 of the ~50 species are bathyal and abyssal, and nearly all the sublittoral, eyed species occur in the northern hemisphere only.

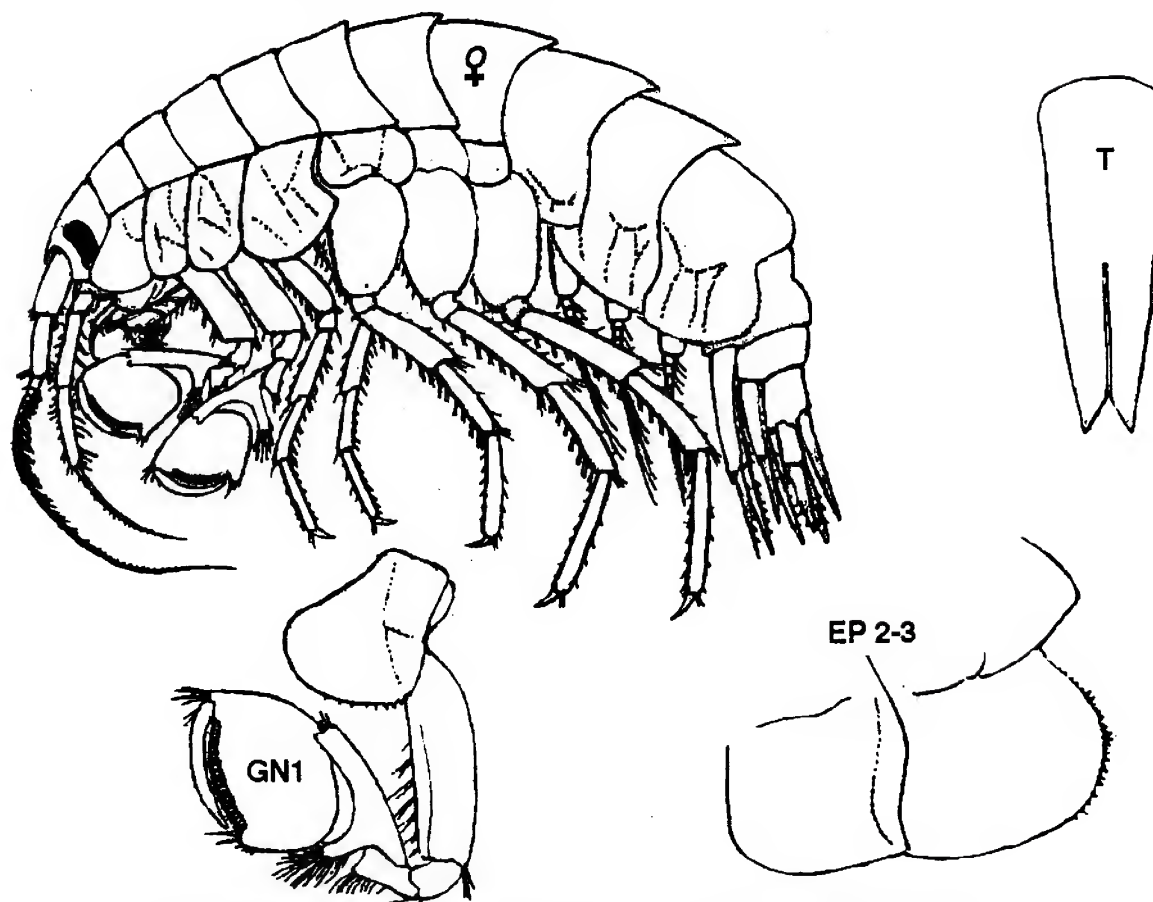


FIG. 1. *Eusirus cuspidatus* (Kroyer, 1845) Female (40 mm) Okhotsk Sea.
(modified from Sars, 1895)

Eusirus cuspidatus Kroyer
(Fig. 1)

Eusirus cuspidatus Kroyer, 1845: 501.—Sars, 1895: 416, pl. 146.—Gurjanova, 1951: 700, fig. 483.—Shoemaker, 1955: 46.—Barnard & Karaman, 1991: 321.

Material Examined: ALASKA: Amchitka I., 100 m, contour of "C" site, near Banjo Pt., trawl, G. Tutmark coll. Sept. 13/1971 - 1 female ov. (slide mt.); Bering Sea, near King I., P. Slattery coll., July 28, 1984 - 1 female br.II (IZ1989-002).

Diagnosis. Female (to 45 mm): The type species has been well described and diagnosed (loc. cit). The following character states have previously been little stressed or utilized in species comparisons:

Eye large, deep, narrowly reniform. Antenna 1 about 10% longer than antenna 2; flagellae weakly or not basally calceolate.

Mandible: molar with small triturating surface; spine row short; palp segment 3 longer than 2. Maxilla 1, inner plate with single apical seta. Maxilla 2, inner plate broad. Maxilliped, inner plate with 3 stout apical spines.

Gnathopods 1 & 2, posterior carpal lobes deeper than distal width of carpus; lobe apically strongly setose.

Peraeopods 3-7 dactyls very short, less than 1/6 length

of respective segment 6. Peraeopods 3 & 4, segment 4 slightly longer than segment 5. Peraeopods 5-7, bases medium broad, convex behind, weakly lobate below.

Uropod 1, peduncle with short distal process but lacking distal hood; rami subequal. Uropod 3, margins setose, spinose. Telson elongate (length ~ 3X basal width), cleft nearly 1/2, notch flared at apex.

Taxonomic and distributional commentary. Material from the southern Chukchi Sea and Bering regions differs in no significant manner from N. Atlantic material illustrated by Sars (1895). This very large species is similar to another large arctic regional species, *E. holmi* Hansen, 1887, in having a posteriorly toothed peraeon segment 7 and short peraeopod dactyls, but differs in its much larger pigmented eyes, much larger and deeper coxal plates, the larger gnathopod 1, shorter and stouter peraeopods, and more deeply cleft telson. Shoemaker (1955) gives regional records of *E. cuspidatus* from Pt. Barrow, Alaska to Kotzebue Sound, and Cook Island, Alaska, from the shallows to depths of 400 m. Like its counterpart species of the antarctic region, *E. perdentatus*, the species is probably an ambush predator that consumes small worms and crustaceans (including other amphipod species) that it seizes by means of its raptorial gnathopods (Klages & Gutt, 1990).

KEY TO NORTH PACIFIC SPECIES OF *EUSIRUS*

1. Pigmented eyes present; pleon plate 3 strongly serrate behind; telson deeply cleft (coastal plain and fiord species) 2.
—Pigmented eyes lacking; pleon plate 3 smooth behind; telson, apex notched (offshore abyssal forms) . 4.
2. Peraeopods 3 and 4, segments 4 & 5 subequal in length; telson cleft ~ 1/2 from apex; animals very large to 40 mm) *E. cuspidatus* (p. 9)
—Peraeopods 3 and 4, segment 4 distinctly longer than 5; telson cleft ~ 1/3 from apex; animals small to medium (5 - 18 mm). 3.
3. Peraeon segment 7 with weak posterior dorsal tooth; peraeopod 7, hind margin of basis weakly incised; maxilliped, palp segment strongly broadened distally *E. hirayamae*, n. sp. (p. 10)
—Peraeon segment 7 lacking dorsal tooth; peraeopod 7, basis straight or slightly convex behind; maxilliped palp, segment 2 normal, much longer than broad *E. columbianus*, n. sp. (p. 10)
4. Peraeopod 5, basis much narrower than peraeopod 7; telson short, subtriangular *E. fragilis*
—Peraeopod 5, basis broad, convex behind; telson elongate *E. bathybius* (Fig. 40, p. 59)

Eusirus longipes Boeck
(Fig. 2)

Eusirus longipes Boeck, 1861: 665.—Sars, 1895: 420, pl. 148(1).—Gurjanova, 1951, 702, fig. 485.—Lincoln, 1979: 402, fig. 191.—Ledoyer, 1982: 235, fig. 159.—Barnard & Karaman, 1991: 321 (part).
non Hirayama 1985: 29.

Taxonomic and distributional commentary. This calceolate, medium-sized (to 18 mm) species occurs widely in the eastern North Atlantic, Mediterranean, and Black Sea regions, on muddy bottoms, in depths of 5-200 m, but not in arctic seas (Gurjanova, 1951; Lincoln, 1979; Ledoyer, 1982).

Hirayama (loc. cit.) identified as this species a 6.5 mm male specimen from the Ariake Sea, Japan. He noted differences between his western Pacific material and the type material from the North Atlantic region, in dorsal peraeonal carination and spination of coxae 2 and 3. These and other differences are here accepted as a basis for recognition of Hirayama's material as a distinct new species (below). The illustration provided by Sars (loc. cit.) is here reproduced for comparison with the new species from Japan.

Eusirus hirayamae, new species
(Fig. 3)

Eusirus longipes Hirayama, 1985: 29, figs. 142-147.—Ishimaru, 1994: 44.

Diagnosis. Male (6.5 mm), Holotype (Hirayama, loc. cit. here designated): Eye deep reniform, strongly pigmented. Antenna 1, flagellum calceolate. Antenna 2, peduncular segment 5 and flagellum calceolate.

Mandible, left lacinia 8-dentate. Maxilliped, palp segment 3 very broad (width ~ length), outer plate tall, columnar.

Gnathopods 1 and 2, carpus and propod broader (thicker) than in *E. longipes*. Peraeopods 3-7, segments 4-6 and dactyl relatively short, thick. Peraeopods 5 and 6, basis broad, rounded behind.

Uropod 1 with stout distal peduncular spine. Uropod 3, rami broadly lanceolate, inner ramus, margins strongly plumose-setose. Telson relatively short (length <2X basal width), cleft ~ 1/4, notch flared distally.

Etymology. The authors are very pleased to name this species in honour of Dr. Akira Hirayama, who first described it, and who has contributed very significantly to knowledge of the amphipod fauna of Japan.

Taxonomic commentary. *Eusirus hirayamae* differs from *E. longipes* Boeck principally in the shorter broader segments of the peraeopods, the short, thick peraeopod dactyls, the stout postero-distal spine of uropod 1, and the presence of a posterior marginal spine on coxal plates 2 and 3.

Eusirus columbianus, new species
(Fig. 5)

Eusirus leptocarpus Wailes, 1931: 41?—Fulton, 1968: 107?—Austin, 1985: 590?

Material Examined: S.E. ALASKA: Boca de Quadra, Head, KEC Sta: 89-2-44 (55° 19.2' N, 130° 27.4' W) 30 m dive, June 27, 1989 - 2 females (5.8 mm) (slide mount). BRITISH COLUMBIA: North-central coast: ELB Stn. H62, Rivers Inlet, 20-30 m, Aug. 10, 1964 - 2 females. C. Levings Stn. 51B-028 (53° 0.58' N, 128° 30.06' W), 52 m, April 4, 1973 - 1 female; Stn. 51B-001, Swanson Bay (52° 00' N, 128° 30' W), Aug. 18, 1975 - 1 female (5.1 mm) (slide mt.); Ibid. Stn. 51B-002, Nov. 18/75 - 1 female; Ibid., Stn. 51B-003, 51 m. - 1 male; Ibid. Stn. 51B-004, 47 m. - 1 female. N. Vancouver I. ELB Stn. P26, Quatsino Sd., Koprino Hbr., 12-16 m dredge, mud shell, woody debris, Aug. 14, 1975. -

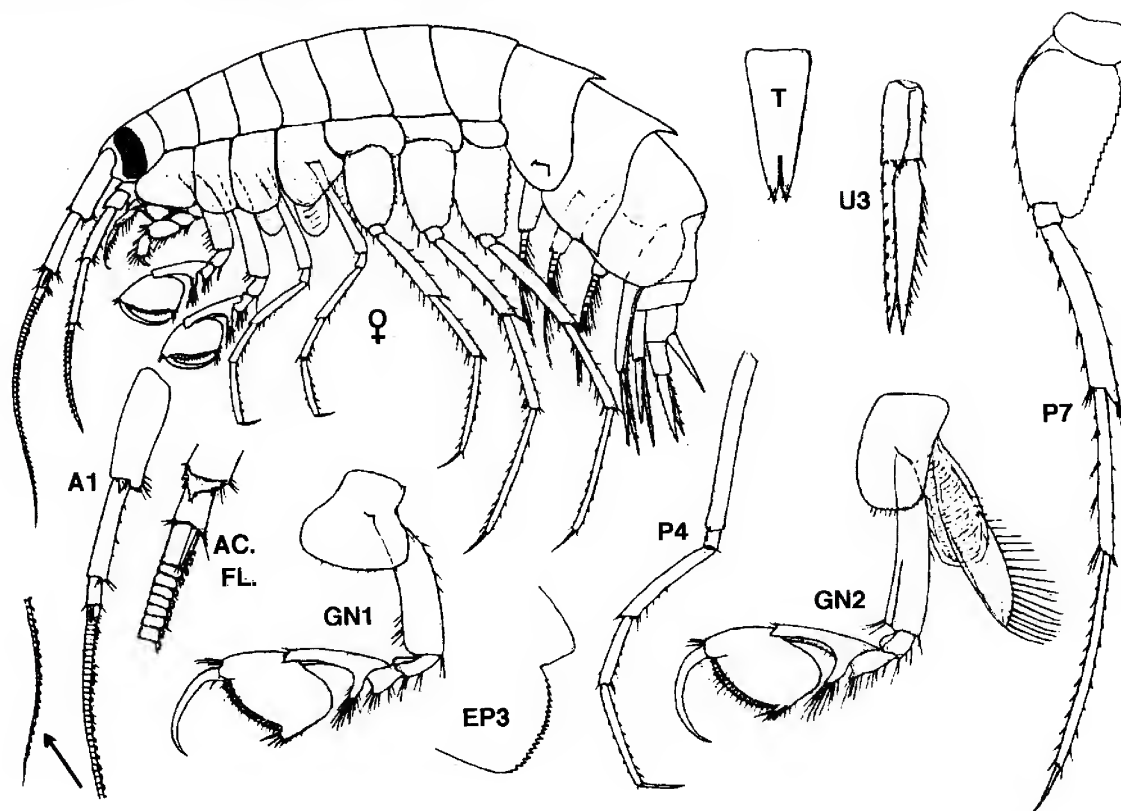


FIG. 2. *Eusirus longipes* Boeck, 1871 Female ov. (13.0 mm) NE Atlantic, to 225 m. (modified from Sars, 1895)

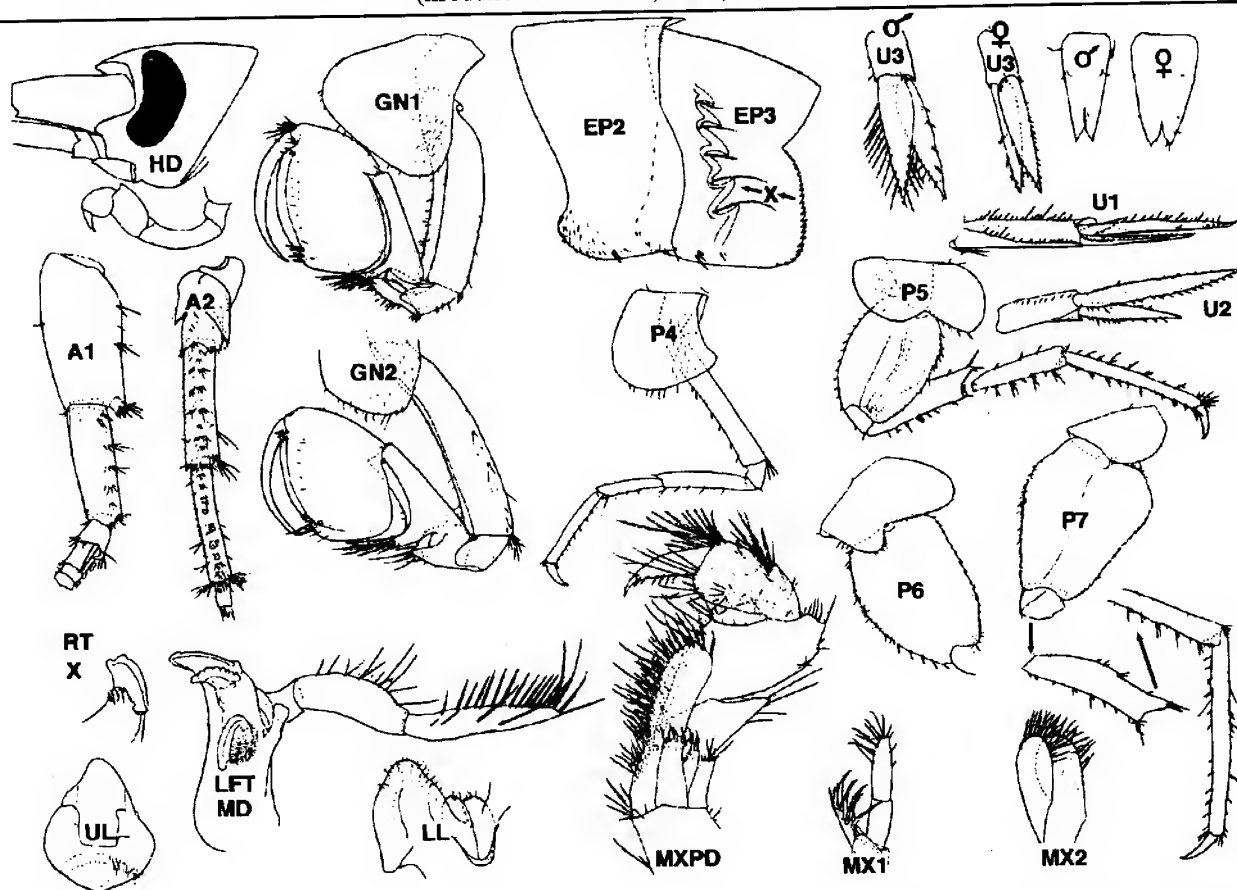


FIG. 3. *Eusirus hirayamae*, new species. Male (6.5 mm) Ariake Sea, Japan. (modified from Hirayama, 1985)

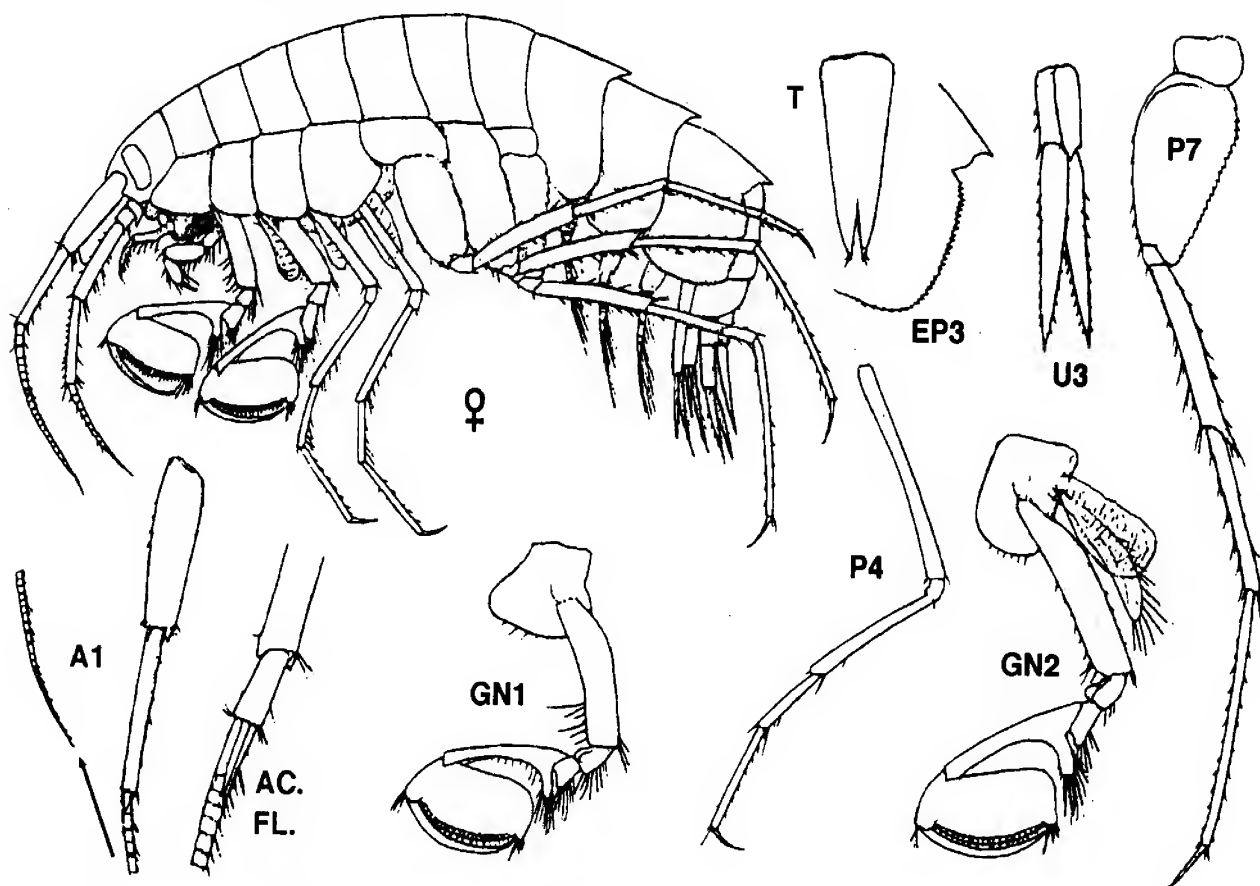


FIG. 4. *Eusirus leptocarpus* Sars, 1895. Female ov (7.5 mm). N.E. Atlantic, to 400 m. (modified from Sars, 1895)

HOLOTYPE female (5.2 mm), CMN Cat. No. pending. ELB Stn. P4, Mouth of Burrard Inlet, nat. dredge, 110 m Nov. 2/77 - 2 females; ELB Stn P6, Off Burrard Inlet, nat. dredge, 150 m., Nov. 3/77 - 1 male, 1 female; ELB Stn. P8, Queen Charlotte Channel, E. of Passage I., nat. dredge, 125 m, Nov. 3/77 - 1 female. S. Vancouver I.: GWO Stn. 153A, Victoria, off Clover Pt., 78 m. Aug. 27, 1976 - 1 female.

Diagnosis. Female (5.2 mm): Body small, slender. Pleon segments 1 and 2 each with low postero-dorsal tooth; peraeon and urosome smooth above. Eye medium, reniform. Antennae stout, relatively short. Antenna 1 little longer than antenna 2; peduncle 3 and flagellum calceolate; accessory flagellum slender, essentially 1-segmented, extending well beyond first flagellar segment. Antenna 2, peduncular segment 5 and basal flagellar segments with anterior marginal calceoli. Calceoli complex, distal element rod-like, elongate.

Mandible, molar weakly tritulative, grinding surface with marginal incomplete ring of short spines; spine row of 4-5 blades; left lacinia 8-dentate; right lacinia bifid-flabellate; palp segment 3 slender, longer than 2 with proximal cluster of 3 longish "A" setae. Maxilla 1, outer plate, inner apical spine flagellate. Maxilla 2, inner plate slightly shorter and broader than outer. Maxilliped, palp segment 2 not broad-

ened distally; outer plate large; inner plate short, with 3 stout apical spines.

Coxae 1-4 medium deep, broad. Coxa 1 strongly broadened distally, hind corner with 2-3 cusps. Gnathopod 2 slightly larger than gnathopod 1; carpal lobes short, relatively broad; propods, postero-distal angle with cluster of 2-3 stout unequal spines.

Peraeopods 3 and 4 slender, 4 slightly the longer; segment 4 ~50% longer than segment 5; dactyls relatively long, slender, > 1/3 length of respective segment 6. Peraeopods 5-7 slender, closely homopodous, differing little in form and length, peraeopod 5 shortest; bases broad, hind margins gently convex or nearly straight, with medium strong serrations; dactyls slender, about 1/3 length of respective propods.

Pleon plate 2, hind corner acuminate. Pleon plate 3 broad, hind margin gently convex, with numerous strong serrations. Pleopods strong, rami about 15-segmented. Uropods 1 and 2 slender, rami strongly serially spinose. Uropod 1, distal peduncular spinose process lacking outer marginal "hood" (as in *E. longipes*); outer ramus slightly (~10%) shorter than inner. Uropod 2, outer ramus short, ~60% length of inner ramus. Uropod 3, rami narrowly lanceolate, outer ramus slightly the shorter, margins spinose.

Telson elongate, narrowing distally, cleft ~1/3. Coxal gills medium, slender sac-like, smallest on peraeopod 7.

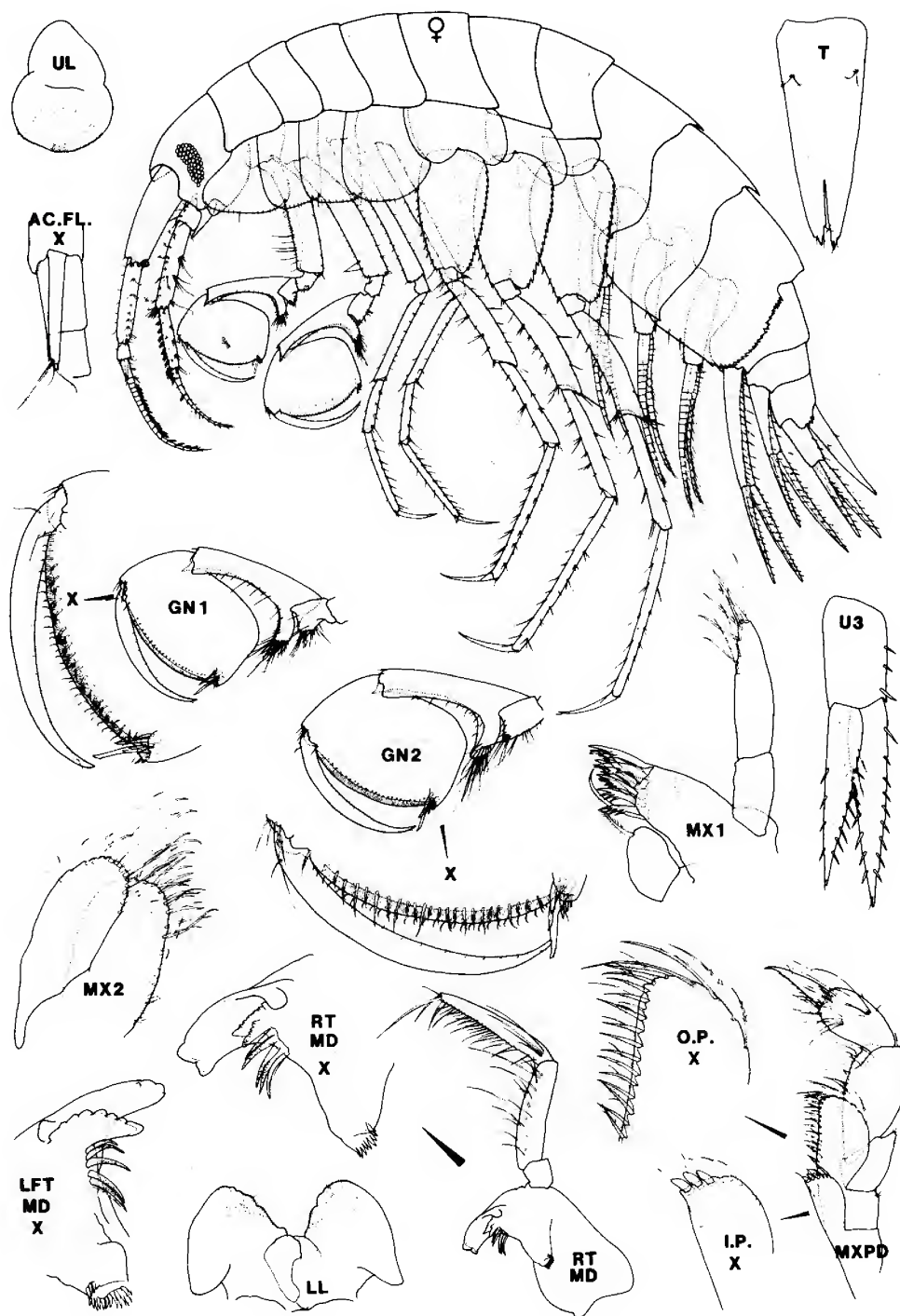


FIG. 5. *Eusirus columbianus*, n. sp. Female (5.2 mm). Koprino Harbour, V. I., British Columbia.

Taxonomic and distributional commentary. *Eusirus columbianus* is known from S. E. Alaska to S. British Columbia, in medium depths (to 125 m). It appears closest to *E. leptocarpus* Sars, 1895 (fig. 4) in the form of the gnathopods, and distinctive notch above the posterior margin of pleon plate 3. However, *E. columbianus* lacks a postero-dorsal

tooth on peraeon segment 3, the peraeopods are shorter and less slender, the dactyls stouter and, in gnathopod 1, the propod is relatively broad, and the carpal lobe broader and apically rounded, not subacute. Previous regional records of *E. leptocarpus* listed by Wailes (1931), (Fulton, 1968), and Austin (1985) are unconfirmed and may be this species.

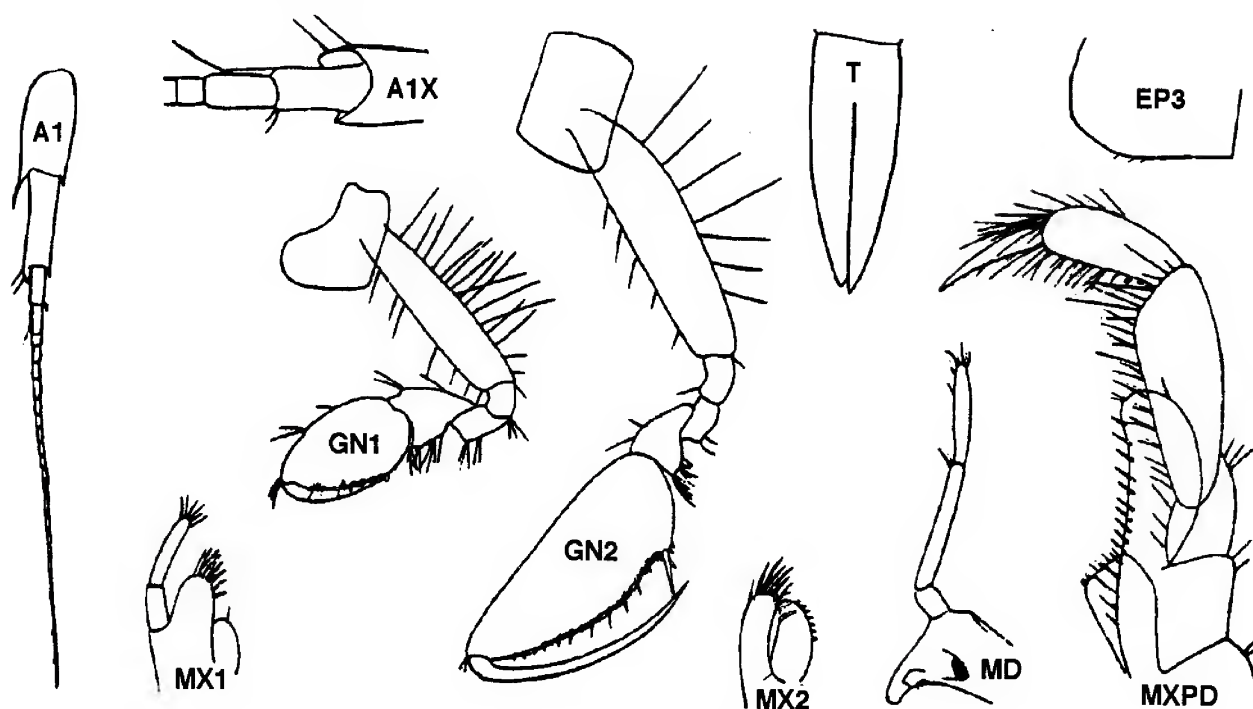


FIG. 6. *Cleonardo macrocephala* Birstein & Vinogradov, 1955. Male (8.0 mm)
Kurile-Kamchatka Trench (modified from Birstein & Vinogradov, 1955)

Cleonardo Stebbing

Cleonardo Stebbing, 1888: 959.—Stebbing, 1906: 345.—Gurjanova, 1951: 704.—Birstein & Vinogradov, 1955: 272.—Barnard, 1969a: 222.—Barnard & Karaman, 1991: 315.

Type species. *Cleonardo longipes* Stebbing, 1888.

Component North Pacific species: *Cleonardo macrocephala* Birstein & Vinogradov, 1955; *C. longipes* Stebbing, 1888; *C. moirae*, new species (p. 15).

Diagnosis: Body not strongly compressed, dorsally smooth or nearly so. Rostrum short to medium. Anterior head lobe rounded to weakly produced. Pigmented eyes lacking. Antennae medium, peduncles and flagella usually calceolate in males and females; distal peduncular segments often lined with brush setae in male. Antenna 1 slightly longer than antenna 2, peduncle 2 usually shorter than 1, both usually with distal process or spine; basal flagellar callynophore weakly (or not) developed in male; accessory flagellum 1-segmented, linear. Antenna 2, peduncular segments 4 and 5 slender, flagellum not shortened.

Upper lip slightly incised below. Lower lip broad, inner lobes weak. Mandible, molar large, triturate; left lacinia 6-8+ dentate, right lacinia bifid; spine row with 4-7 blades; incisor dentate; palp slender, segment 3 variable, occasionally longer than segment 2. Maxilla 1, inner plate with 1-2 apical setae; outer plate with 11 apical spines; palp slender, distal segment longest. Maxilla 2, inner plate broader and shorter than outer plate. Maxilliped palp, segments ordinary; outer plate large; inner plate with 2-3 apical teeth.

Coxae 1-4 regular, medium; coxa 1 broadly rounding, not produced; coxa 4 excavate behind. Coxae 5 and 6 posterolobate. Gnathopod 1 smaller than 2, both strongly subchelate; carpal lobes broad and shallow, or deep and narrow; propods large, posterior margin short, palms oblique, margin spinose, especially near postero-distal angle, having 1-3 clusters of spines into which the tip of the dactyl closes.

Peraeopods 3 and 4 slender, segment 4 distinctly longer than 5, dactyls elongate and simple, or shorter, plumose-setose. Peraeopods 5-7 homopodous, subequal in form and size, not greatly elongate; bases broad, variously lobate; dactyls long.

Pleon plates 1-3 large, regular, not serrate behind. Uropods 1 and 2, rami broadly lanceolate, outer ramus little (10-20%) shorter than inner ramus. Uropod 3, rami broadly lanceolate, outer ramus slightly the shorter, inner margin of inner ramus may be setose. Telson elongate, deeply cleft.

Coxal gills sac-like or plate like, smallest on peraeopod 7. Brood plates on peraeopod 2-4 broad, strap-like on peraeopod 5.

Taxonomic and distributional commentary. The ten described species of *Cleonardo* are bathypelagic (1880-3000+ m), mainly in the North Atlantic, Indian, and North Pacific oceans. The *C. macrocephala* group is distinctive and endemic to the North Pacific region. *Cleonardo longirostris* Chevreux, 1908, an Atlantic species, has been recorded from the northwestern Pacific region by Birstein & Vinogradov (1955, 1960), but is unknown from the North American Pacific study region.

KEY TO NORTH PACIFIC SPECIES OF *CLEONARDO*

1. Gnathopods 1 & 2 subsimilar in size; antenna 1, peduncular segment 1 ordinary *C. longirostris*
—Gnathopod 1 distinctly smaller than 2; antenna 1, peduncular segment 1 with distal hood-like process . 2.
2. Coxa 1 strongly expanded antero-distally; antenna 1, peduncular segment 3 regular, length 1/3-1/2 segment 2; telson lobes narrowing distally *C. macrocephala* (p. 15)
—Coxa 1 slightly expanded antero-distally; antenna 1, peduncular segment 3 very short, ~1/4 length of segment 2; telson lobes narrowing regularly towards apex *C. moirae* (p. 15)

From the standpoint of overall morphology, the 10 world species appear separable into 4 main groups, viz: (1) a relatively primitive, essentially North Atlantic group of *C. appendiculata* (Sars, 1879), *C. microdactyla* Stephensen, 1912, *C. neuvillei* Chevreux, 1908, and *C. longipes* Stebbing, 1888, with the related but more advanced *C. biscayensis* Chevreux, 1908, and *C. maxima*, Birstein & Vinogradov, 1964, occurring also in the Indian Ocean; (2) the single species, *C. spinicornis* Chevreux, 1908, with apomorphic modifications of antenna 1, gnathopods 1 and 2, and bases of pereopod 5-7, also from the Atlantic and Indian oceans; (3) the uniquely deep-plated and setose *C. brevipes* Ledoyer, 1982, known only from the Indian Ocean near Madagascar; and (4) the advanced, globose-headed *macrocephala*-*moirae* species pair, endemic to the North Pacific region.

The two sibling North Pacific species are very similar to each other but differ widely from the other 8 described species of the genus. Unique to the North Pacific pair is the globose form of the head, the antero-distal hood-like process of peduncular segment 1 of antenna 1, the weakly calceolate flagellae of both antennae, the relatively small size of coxa 1, the markedly unequal size of gnathopods 1 and 2, and the short segment 3 of the mandibular palp. They also differ from all but *C. spinicornis* in the relatively long shallow carpal lobes of the gnathopods. Such large and numerous morphological differences are generally recognized at generic (and certainly subgeneric) level in virtually all other gammaridean amphipod families. A revision of the genus *Cleonardo* would therefore seem urgently needed, but is beyond the scope of this limited study.

Cleonardo macrocephala Birstein & Vinogradov
(Fig. 6)

Cleonardo macrocephala Birstein & Vinogradov, 1955: 273, fig. 31.—Birstein & Vinogradov, 1958: 247.—Barnard & Karaman, 1991: 315.

Distributional and taxonomic commentary. This species is a member of the bathypelagic gammaridean amphipod community, sampled in deep closing tows (0-7200 m) over the Kurile-Kamchatka Trench in the northwestern Pacific ocean (Birstein & Vinogradov, loc cit). In most taxonomic features it closely resembles the sibling species *C. moirae* that is described (below) from comparable depths in the eastern North Pacific region.

In addition to the differences provided in the key, *C. macrocephala* may be distinguished from *C. moirae* by:

coxa 1 moderately expanded and strongly rounded anteriorly; propod of gnathopod 2 elongate (length fully twice its depth vs. 1.5 X its depth in *C. moirae*); maxilliped, outer plate large and relatively slender, extending fully half the length of palp segment 2; maxilla 2, inner plate less broadly expanded, width less than twice that of the outer plate; pleon plate 3, hind corner sharply obtuse (vs. sharply rounded in *moirae*); and telson lobes narrowing distally rather than continuously from their basal fusion.

As noted above (p. 15), the *macrocephala* complex stands in considerable morphological isolation from the 3 other major world-wide morphotypes recognized here. Such differences may simply reflect major differences in the kinds of prey organisms or food resources that can be utilized through specialized morphologies. The near-total lack of information on the diets of these species renders such consideration highly speculative. However, the morphological differences might also reflect discontinuities in the deep-water circulation of the world's oceans, non-overlaps that would tend to isolate the North Pacific gene pool and prevent significant genetic influx from adjacent species complexes. Speculatively also, the degree of morphological difference between adjacent populations might also be a measure of the geological time frame or duration of genetic isolation.

Cleonardo moirae, new species
(Fig. 7)

Material Examined: Institute of Ocean Sciences: Off Vancouver Island, over Endeavour Ridge, (47° 58'N., 129° 06' W), June 19-21, 1990: IOS Stn. LC 90-3, tow 006, net 2 1870-1900 m. - 1 female ov. (7.0 mm) Holotype (slide mount), 2 females ov. (7.0 mm) Paratypes, Cat. Nos. pending; IOS Stn. LC 90-3, tow 008, net 2, 1950-1935 m. - 1 male (5.0 mm) Allotype (slide mount), 1 other male (5.0 mm), 1 subadult female (6.0 mm). Ibid, (48° 01'N., 129° 06'W), July 17-19, 1991: IOS Stn. 91-12, VT1, net 1, 0-1888 m - 3 females; Ibid, VT3, net 3, 1985-1787 m. - 1 female. (see also Thomson et al, 1992).

Diagnosis: Holotype female (7.0 mm): Head medium large, somewhat globose. Rostrum short, strongly deflexed. Antennae 1 & 2 subequal, finely calceolate (in males only). Antenna 1, peduncular segment 1 produced antero-distally hoodlike over base of shorter segment 2; segment 2 with 2 sharp antero-distal cusps; peduncle 3 short; accessory flagellum very short; flagellum 20+ segmented. Antenna 2, peduncular segment 5 is 2/3 length of peduncular segment 4;

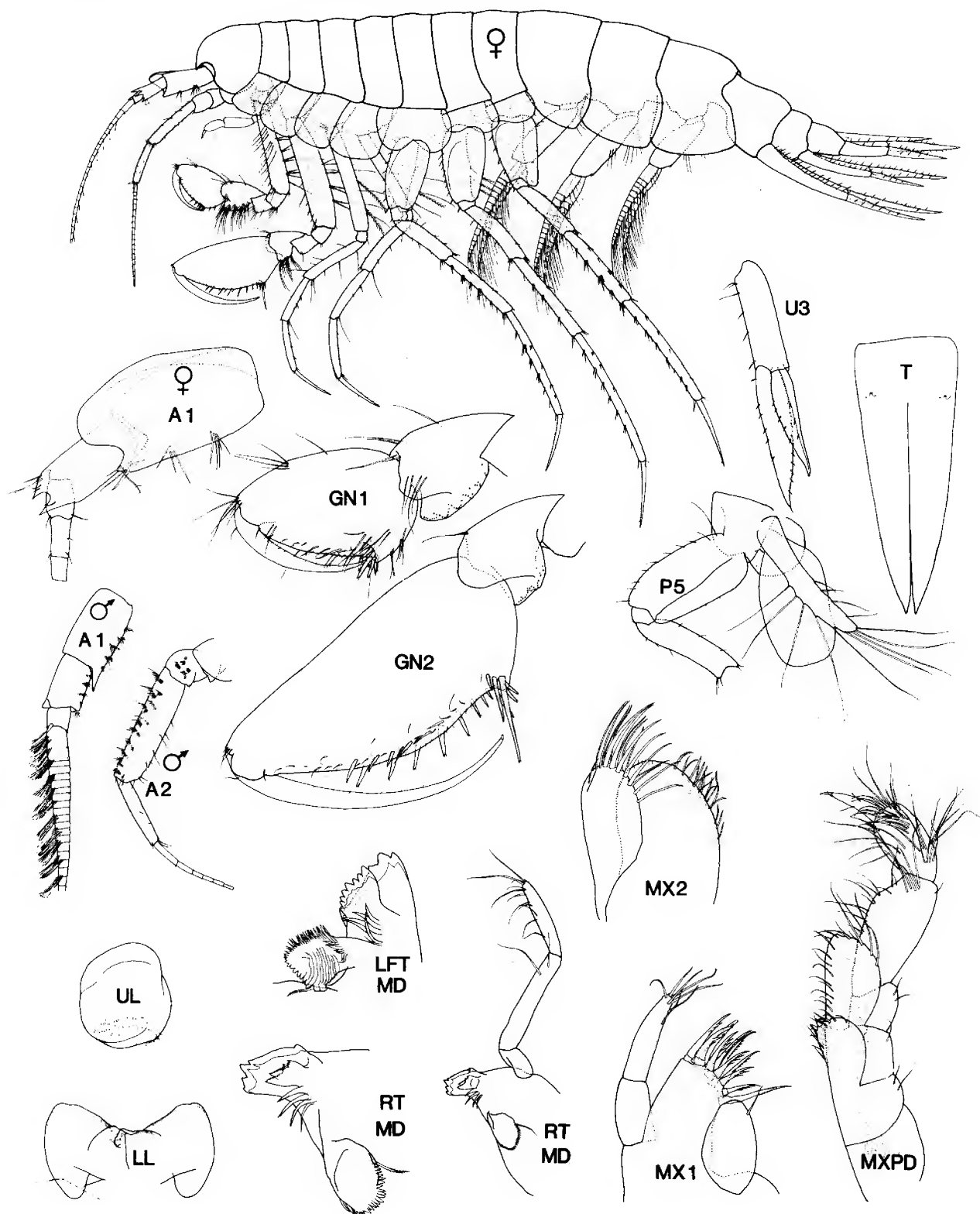


FIG. 7. *Cleonardo moirae*, n. sp. Female ov. (7.0 mm). Off Vancouver I., above Endeavour Ridge. IOC Stn. 90-3 (1900 m); Male (5.0 mm) Stn. 90-3 (1950 m).

flagellum ~ 20-segmented, proximal segment elongate.

Mandible, molar grinding surface ringed by short blades; spine row with 4-5 blades; left lacinia 8-9 dentate; palp not elongate, segment 3 weakly setose, shorter than segment 2. Maxilla 1, inner plate with 1 apical seta. Maxilla 2, inner

plate as long as outer, apex nearly devoid of short setae. Maxilliped ordinary; inner plate with 3 stout apical spines.

Coxal plates 1-4 medium, about as deep as broad; coxa 4 little excavate behind; coxa 5 nearly aequilobate. Gnathopod 1 distinctly smaller than gnathopod 2; posterior margin of

basis lined with setae; carpus shallow, medium, broadly rounded below; propod ovate, palm 2X length of hind margin, outer palmar margin with 2-3 spines proximally and a cluster of 6 spines at palmar angle. Gnathopod 2, carpus shallow, shorter (narrower) than in gnathopod 1; propod slender subovate, palmar margin nearly 3X length of hind margin, proximal 2/3 of inner and outer margins lined with stout spines and a cluster of 6 spines (one spine elongate) at the posterior angle.

Peraeopods 3 and 4 ordinary; segment 4 slightly longer than segment 5; dactyls long, simple. Peraeopods 5-7 homopodous, 6 slightly the longest; bases, hind margins nearly straight, not serrate.

Pleon plates 1-3 broad, hind corners subquadrate, lower margins weakly setose. Uropods 1 and 2, rami medium; inner ramus broadly lanceolate. Uropod 3, rami little longer than peduncle, inner ramus broader and longer than outer ramus, margins weakly spinose. Telson elongate, slender, cleft 3/4 to base; apices sharply acute.

Coxal gills simple, subquadrate. Brood plate on peraeopod 5 strap-like, as long as basis, margins with long setae. Allotype male (5.0 mm): Antennae lacking calceoli; distal peduncular segments of both antennae armed with clusters of brush setae. Antenna 1, peduncular segment 1 with acute postero-distal process; flagellum with weak basal callynophore; distal segments with numerous aesthetascs.

Etymology: This new species is named in honour of Moira Galbraith, Victoria, B. C. who has facilitated examination of much new Pacific pelagic amphipod material.

Taxonomic and distributional commentary. *Cleonardo moirae* is recorded from the IOS stations above, some 300+ km off the outer coast of Vancouver I., B. C., at depths between 1750 and 1950 m. This species is a member of the *macrocephala* group having a large subglobular head, antenna 1, peduncular segment 1 produced anterodistally, and gnathopod propods very unequal in size, with strongly spinose palmar margins. It is distinguished from *C. macrocephala* by the relatively long and shallow carpal lobe of gnathopod 1, the relatively short peduncular segment 2 of antenna 1, and less strongly anteriorly produced margin of

Eusirella Chevreux

Eusirella Chevreux 1908:12.—Birstein & Vinogradov, 1955: 271.—Birstein & Vinogradov, 1960: 224.—Barnard & Karaman, 1991: 317.

Type species. *Eusirella elegans* Chevreux, 1908.

Component North Pacific species: *E. longisetosa* Birstein & Vinogradov, 1960 (tropical western N. Pacific); *E. multicalceola* (Thorsteinson, 1941) (eastern and western North Pacific). A third species, or female morphotype, may be present in material from the eastern North Pacific.

Diagnosis: Body broad and somewhat depressed, as in

physosomatid hyperiids, smooth above. Rostrum short; anterior head lobe rounded, not produced. Pigmented eyes lacking. Antennae medium, calceolate on peduncles and flagella (both sexes), peduncles elongate. Antenna 1 longer than antenna 2; peduncle 2 longer than 1, calceolate; accessory flagellum very short or scale like. Antenna 2, peduncle 4 calceolate, subequal to 5 (shorter than 5 in males); flagellum short, variously longer in males).

Upper lip broadly rounded below. Lower lip, inner lobes distinct. Mandible, molar conical, grinding surface small; spine row with 1-5 blades; left lacinia 6-7 dentate; right lacinia bifid?; palp segments 2 and 3, length subequal. Maxilla 1, inner plate lacking apical setae; outer plate with 9 apical spines; palp short, proximal segment the longer. Maxilliped, palp large, segments 2 and 3 sublinear, not broadened; outer plate large, arcuate; inner plate with minute apical spines.

Coxae 1-4 small, short; coxa 1 weakly produced anteriorly; coxa 4 not excavate behind. Gnathopod 2 larger than 1, both slender, not eusirid in form; propod and carpus variously elongate; palm of propod elongate, margin variously spinose; anterior and posterior margins of bases setose.

Peraeopod 3 and 4 slender, segment 5 shorter than 4, segment 6 and dactyl short, bearing long plumose setae. Peraeopods 5-7 slender, elongate; coxae shallow, aequilobate; bases ovate or sublinear; segments 6 and 7 (dactyl) elongate.

Pleon plates 1-3 rounded below, hind margins not serrate. Pleopods normal, stronger in males. Uropods 1 and 2, rami narrowly lanceolate, outer ramus distinctly (40-50%) shorter than inner ramus; peduncle of uropod 1 lacking antero-distal inter-ramal process. Uropod 3, rami narrowly lanceolate, margins spinose, outer ramus shorter than inner. Telson elongate, deeply cleft, narrowing distally.

Coxal gills medium, sac-like anteriorly, reverse L-shaped, posteriorly smallest on peraeopod 7. Brood plates long, strap-like.

Taxonomic commentary. Two species of *Eusirella* have been recorded from the N. Pacific region but only *E. multicalceola* is known from offshore waters of the North American Pacific coast. The genus is plesiomorphic in the calceolate antennae, slender gnathopods, and deeply cleft telson, but in most character states of the mouthparts and appendages it is strongly apomorphic (see also Fig. 33).

Five species have been described, three of which (*E. elegans* Chevreux, 1908; *E. heterochela* Birstein and Vinogradov 1964, and *E. flagella* Andres, 1982, have been recorded from Atlantic and Antarctic regions. Barnard (1964) suggested that *E. elegans* Shoemaker, 1945, exhibits several character states distinct from those of *E. elegans* Chevreux, and may be a full species of its own.

Eusirella longisetosa Birstein & Vinogradov
(Fig. 8)

Eusirella longisetosa Birstein & Vinogradov, 1960: 224, fig. 30.—Barnard & Karaman, 1991: 318.

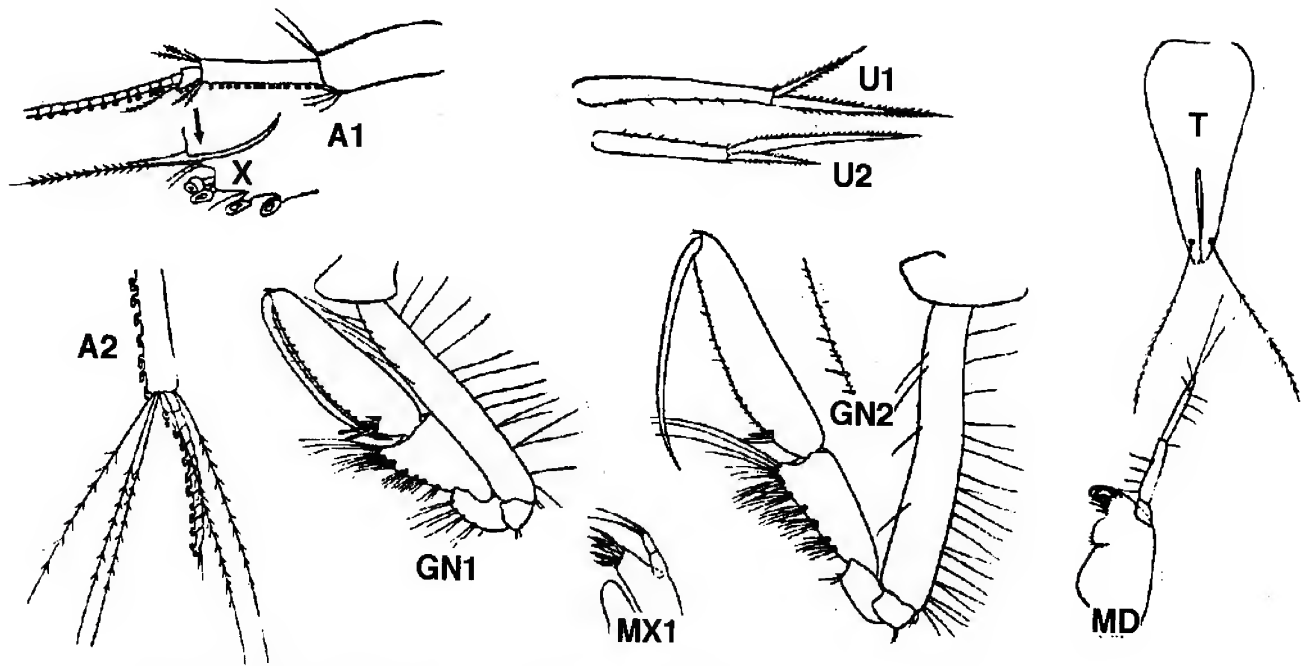


FIG. 8. *Eusirella longisetosa* Birstein & Vinogradov, 1960. Male (7.3 mm). Warm-temperate N. Pacific, off S. E. Japan (After Birstein & Vinogradov, 1960)

KEY TO NORTH PACIFIC SPECIES OF *EUSIRELLA*

1. Antennal peduncles with dense masses of calceoli; antenna 1, peduncular segment 3 regular, short; gnathopod 2, propod much longer than in gnathopod 1; dactyl extending little more than half total lower margin of propod; telson cleft 3/4 length, apices normal *E. multicalceola* (p. 18)

—Antennal peduncles with ordinary numbers of calceoli; antenna 1, peduncular segment 3 produced under first flagellar segment; gnathopod 2, propod little longer than in gnathopod 1; dactyl extending very nearly along the entire lower margin; telson cleft 1/3, apices each with single long seta . . . *E. longisetosa* (p. 17)

Taxonomic and distributional commentary. The partial description and illustration of this species is based on a single male specimen (7.3 mm) taken in a vertical tow (0-8500 m) off the southeastern coast of Japan (Birstein & Vinogradov, loc. cit.). *E. longisetosa* has not yet been taken in North American Pacific waters. It differs markedly from the female of *E. multicalceola* Thorsteinson in character states of the antennae, gnathopods, and telson, as outlined in the key (above). Additional differences are as follows:

Antenna 1, peduncular segment 3 produced posterodistally behind flagellar segment 1, hind margin with 4 calceoli.

Gnathopod 1, coxa, anterodistal corner slightly produced, rounded; basis slender, elongate; propod, palmar margin lined with evenly spaced short slender spines; postero-distal angle with cluster of 4 stout spines. Gnathopod 2, basis posteriorly lined throughout with longish setae; propod, palmar margin lined with slender spines of irregular length; postero-distal angle with cluster of 3 stout spines.

Mandible, spine row with 5-6 blades; palp segment 3 slightly longer than segment 2. Maxilla 1, palp segments 1 and 2 subequal in length; outer plate with 9 apical spines; inner plate apically bare.

Uropods 1 and 2, outer ramus short, < 1/2 length of inner ramus, margins with numerous serial pairs of short spines.

Eusirella multicalceola (Thorsteinson) (Figs. 9, 10, 11)

Gracilipes multicalceolus Thorsteinson, 1941: 85, pl. 7, figs. 71-77.—Birstein & Vinogradov, 1955: 271, fig. 30.

Eusirella multicalceola—Birstein & Vinogradov, 1958: 247.—Birstein & Vinogradov, 1960: 224.—J. L. Barnard, 1964: 321, figs 6, 7.—Kamenskaya, 1981a: 101.—Barnard & Karaman, 1991: 318.

Material Examined: BRITISH COLUMBIA: Queen Charlotte Islands: off Kunghit I. (52°00.39'N, 131°23.97'W to 52°00.55'N, 131°30.90'W) IKMT, 0-510m, RBCM/CMN Stn 91-1-03, Mar. 19/91 - 2 females; off Tasu Sd (52°38.72'N, 132°05.79'W to 52°38.31'N, 132°09.90'W) IKMT 0-520m, RBCM/CMN Stn. 91-1-09, Mar. 20, 1991 - 1 male, 1 female. Ibid., over Barkley Canyon, J. P. Tully Cruise, #1990-12, IKMT 450-525m, December, 1990 - 2 females. off Hippa I. (53°30.39'N, 133°26.35'W to 53°34.55'N, 133°30.20'W) IKMT 0-660m, RBCM/CMN Stn. 91-1-12, Mar. 22/91. - 3 females.

Off outer Coast of Vancouver I., over Endeavour Ridge, (48°01'N, 129°06'W) IOS Stn 91-12, Tow 3, net 3, 1985-1787 m. - 1 female ov. (11.0) mm. 1 br. young; Stn. 91-12,

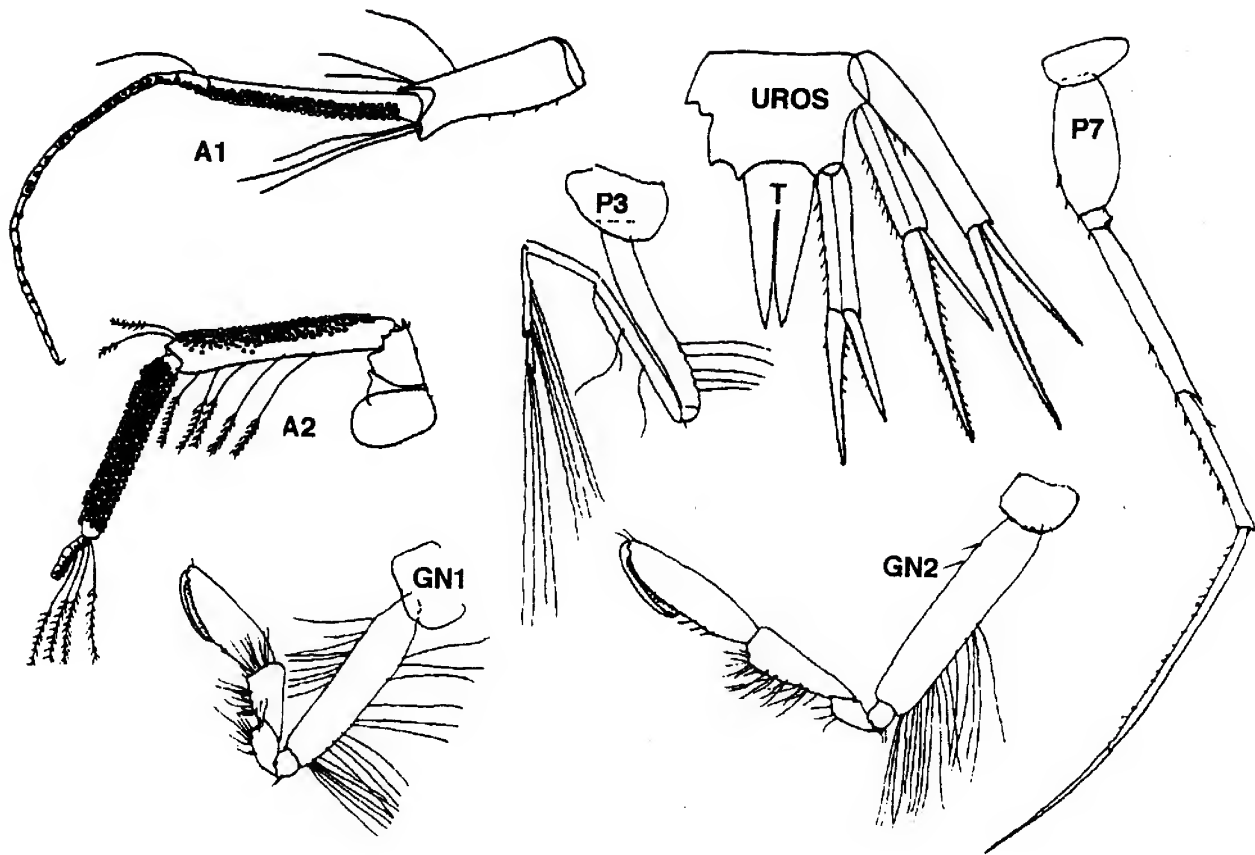


FIG. 9. *Eusirella multicalceola* (Thorsteinson, 1941) Male (11.0 mm)
Gulf of Alaska, 1000-1200 m. (modified from Thorsteinson, 1941).

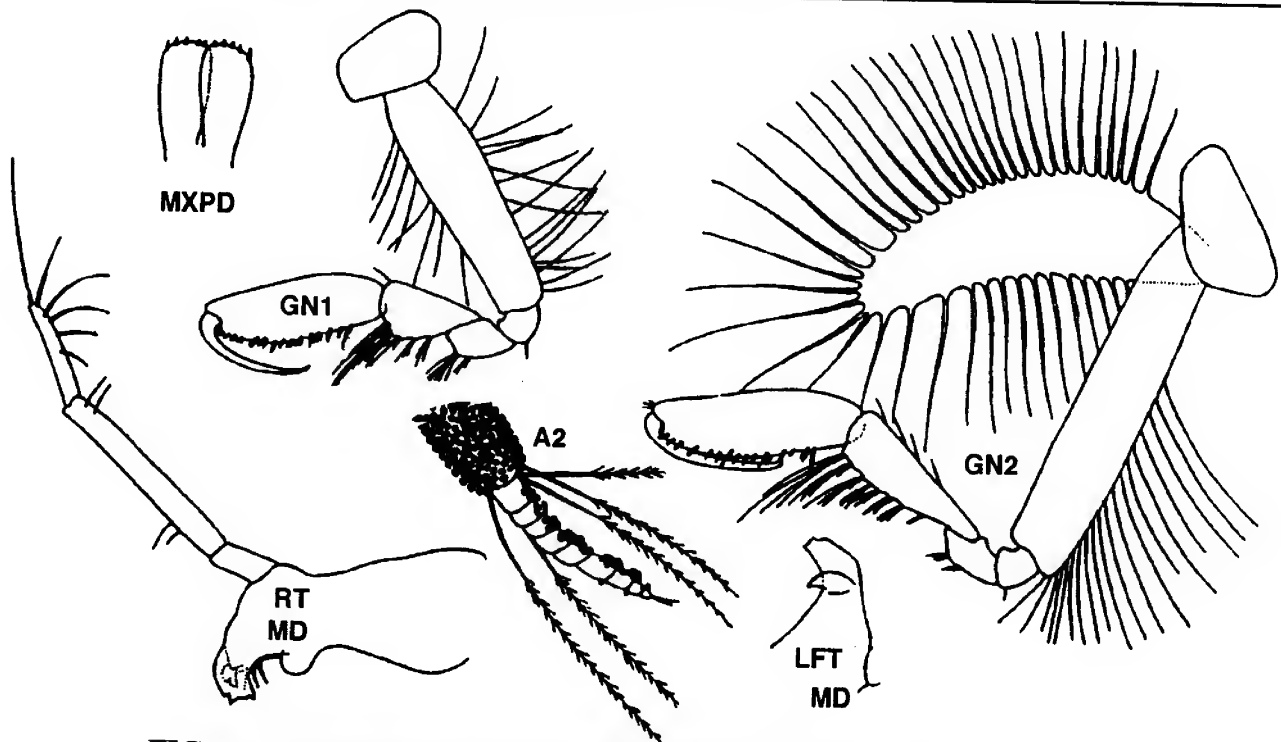


FIG. 10. *Eusirella multicalceola* (Thorsteinson, 1941). Female (9.0 mm)
Kurile-Kamchatka Trench (modified from Birstein & Vinogradov, 1955)

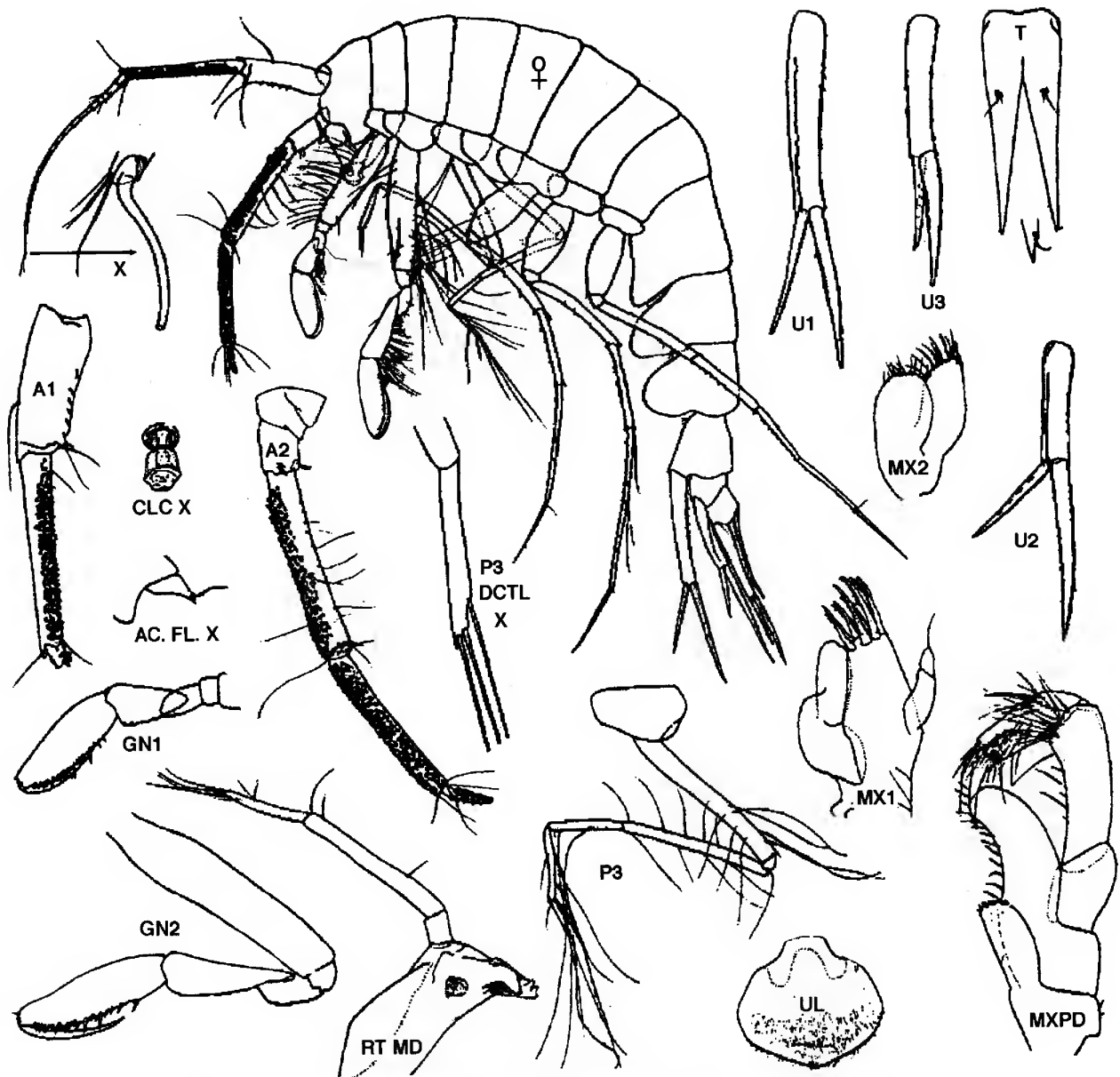


FIG. 11. *Eusirella multicalceola* (Thorsteinson). Female? (8.0 mm)
Off Queen Charlotte Islands, 3200 m. (modified from Barnard, 1964)

Tow 4, Net 3, 2306-1925 m. - fem. br. III (10.2 mm); Stn. 91-12, Tow 2, Net 1, 0-1900 m. - 1 male (7.2 mm).

Diagnosis. Male (8.0 mm): The male of the species has been described and figured by Thorsteinson, 1941. No female-defining characters were treated by Barnard, 1964, or by Birstein & Vinogradov (1955) and in our view a bone fide female has yet to be treated clearly as such. Female (10.0 mm): Differs from the male in its larger size, broader body, longer and less calceolate antennae, more elongate gnathopod propods and dactyls, more elongate pereopods, and presence of strap-like brood plates on pereopod segments 2-5.

Antenna 1, peduncle 3 slender, elongate (2 X segment 1) Antenna 2, peduncular segments 4 and 5 slender, subequal, anterior margins moderately heavily but not densely calceolate (as in male); flagellum with 8 short segments (remainder

broken off), proximal 3 each with single calceolus; accessory flagellum as illustrated by Barnard, 1964 (see Fig. 11).

Coxa 1 truncated. Gnathopod propods very slender, elongate; gnathopod 1 smaller than gnathopod 2, propod of gnathopod 1 about 2/3 length of 2, dactyls long, closing along almost entire lower margin, bordered by spine cluster at the postero-distal angle, near carpus.

Coxal gills present on pereopods 2-7, slender sac-like on 2-4, reverse L-shaped on 5 and 6, small, on pereopod 7. Brood plates medium; long, strap-like on pereopod 5.

Taxonomic and distributional commentary. Birstein & Vinogradov (1958) include this species (along with *Rhachotropis natator*) in a northern group of pelagic gammarids from collection localities of the Institute of Oceanography from off eastern Japan to the Kamchatka peninsula (north of 37-40°), in depths ranging from 100 - 2000+ m.

Western Pacific Genera and Species

Of the ten genera of family Eusiridae represented in the North Pacific ocean, five of these (*Harcledo*, *Stenopleura*, *Pareusirogenes*, *Eusiropsis*, and *Eusirogenes*) are known to date only from Asiatic offshore localities, well outside the present study region. One of these (*Pareusirogenes*) has not yet been recorded elsewhere in the world (see also Table III, p. 52). However, in view of the limited amount of collecting and/or analysis of meso- and bathypelagic gammaridean amphipods from North American Pacific waters, published upon to date (p. 4), and the broad distributions of some species, most (if not all) of these genera may yet be recorded from the eastern North Pacific region. These genera are therefore included in the key (p. 7) and annotated briefly (below), and morphological features of representative western Pacific species are shown in the Appendix (pp. 57-59, Figs. 35-39).

Harcledo J. L. Barnard
(see Fig. 35, p. 57)

Harcledo J. L. Barnard, 1964: 60.—Barnard & Karaman, 1991: 323.

Meteusiroides Pirlot, 1934: 602.—Birstein & Vinogradov, 1955: 269, fig. 29.

Taxonomic commentary. *Harcledo curvidactyla* (Pirlot) was first described from the North Pacific as *Meteusiroides plumipes* Birstein & Vinogradov (loc. cit.) from mesopelagic waters of the Kurile-Kamchatka Trench. The genus *Harcledo* is primitive in that the single known species possesses pigmented eyes, relatively unmodified mouthparts, broad but unproduced coxal plates; regular (non-eusirid) gnathopod carpi; broad, lobate bases of peraeopods 5-7; subacute, unserrated pleon plate 3; marginally setose rami of uropod 3; and long, deeply cleft telson. The dorsally smooth body, and distally narrowing gnathopod propods with palmar margins nearly horizontal are distinctive, more apomorphic features of the genus.

Stenopleura Stebbing
(see Fig. 36, p. 57)

Stenopleura Stebbing, 1888: 949.—Birstein & Vinogradov, 1958: 243.—Ibid, 1960: 220.—Barnard & Karaman, 1991: 340.

Taxonomic commentary. *Stenopleura atlantica* Stebbing, 1888, has been recorded from the North Pacific region by Birstein and Vinogradov (loc. cit.) from warmer mesopelagic waters southeast of Japan. Whereas the genus entrains some plesiomorphic character states such as pigmented eyes, regular (non-eusirid) gnathopod carpi, and unmodified pleon plates, it is more advanced than *Harcledo* in its smaller coxal plates (coxa 1 sharply produced); more specialized mouthparts; spinose (not setose) margins of the rami of uropod 3; and short, apically notched telson.

Pareusirogenes Birstein & Vinogradov
(see Fig. 37, p. 58)

Pareusirogenes Birstein & Vinogradov, 1955: 266, fig. 27.—Ibid, 1958: 246.—Barnard & Karaman, 1991: 333.

Taxonomic commentary. *Pareusirogenes carinatus* was described by Birstein and Vinogradov (1955, 1958) from deep net hauls (0-3000 m) over the Kurile-Kamchatka Trench and in the Sea of Okhotsk. The genus is characterized by weakly eusirid gnathopods 1 and 2 in which the posterior margin of the carpus is elongate, shallow and heavily fringed with setae, the propod palmar margins are strongly oblique, and uropod 3 has a single large marginally serrate ramus. Many of the body parts (including the antennae, distal segments of the peraeopods, uropods 1 and 2, and telson) have not yet been described or figured. The genus is the most primitive of *Eusirus*-like genera in the relatively unmodified mouthparts and broad posteriorly convex bases of peraeopods 5-7.

Eusiropsis Stebbing
(see Fig. 38, p. 58)

Eusiropsis Stebbing 1897: 39.—Stebbing 1906: 343, figs. 80, 81.—Birstein & Vinogradov, 1958: 246.—Ibid, 1960: 223.—Barnard & Karaman, 1991: 319.

Taxonomic commentary. Birstein & Vinogradov (loc. cit) recorded *E. riisei* Stebbing, 1897, on the basis of 20 specimens (7-12 mm) from closing tows, mostly of less than 1000 m. in depth, at a dozen oceanographic stations off southeastern Japan. The genus differs from all others (with eusirid gnathopods), in having a combination of nearly smooth dorsum, elongate strongly calceolate antennae, shallow coxal plates, short cryptic gnathopod carpi, slender distally plumose-setose peraeopods, heavily setose rami of uropod 3, and relatively short, shallowly cleft telson.

Eusirogenes Stebbing
(see Fig. 39, p. 59)

Eusirogenes Stebbing 1904: 15.—Stebbing, 1906: 728.—Birstein & Vinogradov, 1955: 259, fig. 26.—Ibid, 1958: 246.—Barnard & Karaman, 1991: 318.

Taxonomic commentary. The genus is superficially similar to *Eusirus* but the propod of gnathopod 1 is distinctly larger than in gnathopod 2, the mouthparts are more specialized, coxae 1-4 are markedly unequal in size and depth, the bases of peraeopods 5-7 are markedly heteropodous, and the telson is usually less deeply cleft. The northerly records of *Eusirogenes homocarpus* Birstein & Vinogradov (loc. cit.) in the western North Pacific, indicate that this species, or a sibling counterpart, is likely to occur in deep offshore waters of the North American Pacific coast.

Rhachotropis Smith

Rhachotropis Smith, 1883: 222.—Stebbing, 1906: 847.—Shoemaker, 1930: 317.—Gurjanova, 1951: 706.—Barnard, 1969a: 229.—Ledoyer, 1982a: 235.—Barnard & Karaman, 1991: 337.

Gracilipes Holmes, 1908: 526.

Type Species. *Oniscus aculeatus* Lepechin, 1780.

Component North Pacific species. (Alaska to Baja California): *Rhachotropis aculeata* (Lepechin, 1780); *R. inflata* (G. O. Sars, 1892), *R. oculata* (Hansen, 1888), *R. minuta*, new species; *R. helleri* (Boeck, 1871); *R. macropus* Sars, 1895; *R. boreopacifica*, new species, *R. conlanae*, new species; *R. calceolata*, new species; *R. ludificor*, J. L. Barnard, 1967a; *R. clemens* J. L. Barnard, 1967a; *R. barnardi*, new species; *R. multesimus* J. L. Barnard, 1967; *R. americana*, new species; *R. grimaldi* (per Gurjanova, 1955); *R. inflata* Sars, 1883; *R. natator* (Holmes, 1908), and *R. distincta* (Holmes, 1908). *R. gubilata* J. L. Barnard, 1964, a relatively primitive bathyal species originally described from the Gulf of Panama, is recorded from the Cascadia abyssal plain off Oregon and is therefore included in the morphological analysis (pp. 51-52) and phenogram (Fig. 34). The identity of *R. cervus* Barnard, 1964, in the Baja California region is uncertain, and not included in the analysis or keys of this study.

Diagnosis: Body usually carinate-mucronate on pleon mid-dorsally and laterally, often also on posterior peraeonal and first urosomal segments. Rostrum medium, strong to short; anterior head process usually acutely produced. Pigmented eyes present in neritic species, large, often nearly meeting mid-dorsally, lacking in bathyal species. Antennae medium, stout, subequal, peduncles strong, often calceolate, distal ends often armed with longish "bottlebrush" sensory setae. Antenna 1, accessory flagellum very short, 1-segmented, apex spinose and/or setose, or scalelike, or lacking. Antenna 2 often calceolate on peduncle and flagellum in female.

Upper lip rounded below, epistome not produced. Lower lip, outer lobes broad, inner lobes strong. Mandible: molar columnar, grinding surface reduced; spine row with 3-8 blades; left lacinia 6-7 dentate; palp strong, segment 3 usually longer than segment 2. Maxilla 1, outer plate 9-dentate; inner plate with 1-4 apical setae; palp stout, normally 2-segmented. Maxilla 2, inner plate broader, facial setae reduced to single strong inner marginal plume, or lacking. Maxilliped, palp powerful; plates reduced, inner plate, apical spines present.

Coxal plates small, shallow, slightly increasing in size posteriorly. Coxa 1 strongly and narrowly produced anteriorly; coxa 4 weakly (or not) excavate behind. Gnathopods powerfully subchelate, subequal, raptorial; propod broadly ovate, palmar margin smoothly convex, lined on either side with closely set stiff setae, but with stout spines only at posterior angle; carpus short, posterior lobe deep.

Peraeopods large, stout, spinose, raptorial, dactyls medium to elongate, nails short. Peraeopods 3-4, segment 4 variously shorter than segment 5 (subequal in type species), usually markedly shorter in peraeopod 3. Peraeopods 5-7 elongate. Peraeopods 5 and 6 often subequal in length, but bases subsimilar in form. Peraeopod 7 distinctly largest, basis usually larger and differing in form from that of peraeopods 5 and 6.

Pleon plate 3 rounded and usually strongly serrated behind. Uropods 1 and 2, rami slender, lanceolate (apices lacking terminal spines); outer ramus the shorter. Uropod 3, rami subequal, broadly lanceolate, inner margins spinose, also setose in primitive species. Telson elongate, narrowing distally; apex variously cleft; lobes often slightly asymmetrical, rarely fused to entire plate; basally with pair of elongate "bottle-brush" sensory setae.

Coxal gills large, weakly pleated, smallest on peraeopod 7. Brood plates broad, margins setose.

Taxonomic and distributional commentary. On a world-wide basis, about 60% of the ~50 described species of *Rhachotropis* occur in northern oceans, including the Mediterranean Sea, and the remainder in Indian, Australian and Antarctic waters. Only about one-third of the species are sublittoral and have pigmented eyes; most are epibenthic bathyal and abyssal, lacking pigmented eyes, and a few are bathypelagic. Most of the sublittoral (eyed) species have been found in arctic and arctic-boreal regions of the North Atlantic and North Pacific oceans. In the North Atlantic, the species occur variously southward to the Mediterranean region in the east, and to the Cape Cod region in the west. In the North Pacific they are dominant along the North American coastal plain south to Baja California, and penetrate the western Pacific south to the Sea of Japan. Although the genus *Rhachotropis* may be considered cosmopolitan, most bathyal and abyssal species are recorded from the northern hemisphere; their distributions are based on very few records, perhaps suggesting a significant degree of regional endemism within the deep-water forms.

Morphologically, the sublittoral forms tend to retain plesiomorphic character states, whereas the bathyal species trend to apomorphies such as total fusion of telson lobes and loss of antennal calceoli. The bathypelagic species are most apomorphic in extreme elongation of peraeopods and dactyls, reduction of coxal plates, and elongation of antennae.

The *Rhachotropis* fauna of the North Pacific region contains a mixture of sublittoral, bathyal, and bathypelagic species of which 19 species are included in the regional key and species analysis (p. 23). Of these, 8 are fully described and/or figured, based mainly on material at hand. Descriptive remarks and/or figures of the other species, based on the literature, are provided in several instances.

These 19 North Pacific species of *Rhachotropis* may be grouped on a phyletic-ecological basis, as follows: (1) a primitive, strongly rostrate and dorsally toothed group that includes the monotypic *R. aculeata* (Lepechin) of arctic

KEY TO NORTH PACIFIC SPECIES OF *RHACHOTROPIS*

1. Pigmented eyes present 2.
—Pigmented eyes lacking 11.
2. Peraeon segments 6 and 7 with dorsal and dorso-lateral teeth; urosome 1 with 2 dorsal teeth; peraeopods 5 and 6, hind margin of basis with strong posterior tooth *R. aculeata* (p. 24)
—Peraeon segments 6 and 7 with distinct tooth mid-dorsally only, or all teeth lacking; urosome 1 with single dorsal tooth (or none); peraeopods 5 and 6, basis convex behind, without strong posterior tooth 3.
3. Pleon segment 3 with mid-dorsal tooth; telson elongate ($>> 2X$ basal width) 4.
—Pleon segment 3 lacking mid-dorsal tooth; telson relatively short ($\sim 2X$ basal width, or less) 7.
4. Peraeopods 3 and 4, dactyls ordinary (length $< 2/3$ segment 6); telson deeply cleft ($> 1/3$ its length) . . . 5.
—Peraeopods 3 and 4, dactyls elongate (\sim segment 6); telson with short apical cleft 6.
5. Peraeopod 7 elongate ($>>$ peraeopod 6); telson deeply cleft ($\sim 1/2$ length) *R. macropus* (p. 26)
—Peraeopod 5 regular (slightly $>$ peraeopod 6); telson cleft $\sim 40\%$ of its length *R. helleri* (p. 26)
6. Pleon segment 3 with strong dorsal and dorso-lateral mucronations *R. boreopacifica* (p. 29)
—Pleon segment 3 lacking dorsal and dorso-lateral mucronations *R. barnardi* (p. 29)
7. Peraeon segment 7 with mid-dorsal tooth 8.
—Peraeon segment 7 lacking mid-dorsal tooth 9.
8. Peraeopods 3 and 4, dactyls long (\sim segment 6); rami of uropod 3, inner margins setose *R. oculata* (p. 33)
—Peraeopods 3 and 4, dactyls short ($\sim 1/2$ segment 6); uropod 3 rami, inner margins spinose *R. minuta* (p. 35)
9. Pleon segments 1 and 3 each with strong dorso-lateral tooth and ridge *R. inflata* (p. 33)
—Pleon segments 1 and 3 lacking dorso-lateral tooth and ridge 10.
10. Peraeopods 3 and 4, dactyls short, thick, $< 1/2$ segment 6; S. E. Alaska *R. conlanae* (p. 37)
—Peraeopods 3 and 4, dactyls elongate, length \sim segment 6; Gulf California *R. luculenta* (p. 37)
11. Urosome 1 with mid-dorsal tooth or mucronation 12.
—Urosome 1 lacking mid-dorsal tooth 14.
12. Pleon segment 3 with dorsal tooth; coxa 1 weak; antenna 1, ped. segment 3 long . . . *R. distincta* (p. 43)
—Pleon segment 3 lacking dorsal tooth; coxa 1 produced; antenna 1, peduncular segment 3 short . . . 13.
13. Antennae strongly calceolate; telson deeply cleft; gnathopod carpal lobes broad . . . *R. calceolata* (p. 26)
—Antennae not calceolate; telson notched at apex; gnathopod carpal lobes narrow *R. clemens* (p. 32)
14. Coxa 1 small, short; telson elongate, shallowly notched apically 15.
—Coxa 1 strongly produced anteriorly; telson deeply cleft ($> 1/3$) 16.
15. Peraeopods 5-7, basis with posterior cusp; pleon 3 strongly toothed, dorso-laterally . . . *R. gubilata* (p. 24)
—Peraeopods 5-7, basis smooth behind; pleon 3 weakly cusped, mid-dorsally only *R. natator* (p. 46)
16. Pleon segment 3 lacking dorsal tooth; peraeopod 6, basis broad; rostrum large *R. ludificor* (p. 37)
—Pleon segment 3 with mid-dorsal tooth; peraeopod 6, basis narrow; rostrum short, small 17.
17. Peraeopod 7, basis narrow, straight; pleon plate 3 smooth behind *R. multesimis* (p. 40)
—Peraeopod 7, basis medium broad, hind margin convex; pleon plate 3 serrate behind 18.
18. Head and peraeon with low dorsal tubercles; pleon 3, dorso-lateral tooth strong *R. grimaldi* (p. 40)
—Head and peraeon segments smooth above; pleon 3, dorso-lateral cusp weak *R. americana* (p. 40)

waters and possibly the abyssal *R. gubilata*; (2) a more advanced northern sublittoral *macropus* group that includes *R. boreopacifica*, n. sp., *R. barnardi*, n. sp., and *R. clemens* Barnard, 1967 along the North American coast, and *R. helleri* (Boeck) and *R. macropus* Sars in the western North Pacific; (3) a further advanced sublittoral subarctic *oculata-inflata* group that includes *R. conlanae*, n. sp., and *R. minuta* n. sp. of the North American coast; (4) a bathyal complex apparently endemic to the eastern North Pacific region, that includes *R. ludificor*, *R. calceolata*, a group in which the sublittoral *R. luculenta* from the Gulf of California may also be placed; (5) a bathyl *R. grimaldi* group (Gurjanova type) that includes *R. americana* and *R. multesimus* of the North American coast; and (6) a bathypelagic offshore group that comprises *R. natator* and *R. distincta*, with specialized character states, formerly recognized in the genus *Gracilipes* Holmes, 1908. *Gracilipes* may yet prove to be a valid genus, but its determination requires detailed study of the entire range of deep sea species and materials not available to us here.

***Rhachotropis aculeata* (Lepechin)**
(Fig. 12)

Rhachotropis aculeata Sars, 1895: 424, pl. 149.—Shoemaker, 1920: 14E.—Gurjanova, 1951: 707, fig. 491.—Shoemaker, 1955: 46.—Barnard & Karaman, 1991: 339.

Material Examined. CHUKCHI SEA: Stn AHPR -off Wainwright, Alaska, otter trawl, 35 m., gravel, P. Slattery coll. 1984 - 1 female ov (31 mm) (fig'd), 9 other females. CMN Acc. No.; Ibid. 25 m dive, P. slattery coll. Aug. 1984. 1 male; Off Cape Thompson, 26 m. S.E. Point Hope 35 m trawl, P. Slattery coll., August, 1984 - 1 female (br. I).

Diagnosis. Female (to 40 mm): Body large, broadest in mid peraeon. Peraeon segments 1-5 mid-dorsally rugose, segment 6 and 7 with acute dorsal, dorso-lateral, and lateral processes. Pleon segments 1-3 each with strong mid-dorsal tooth, and small anterior cusp and strong dorsolateral tooth. Urosome 1 with bidentate mid-dorsal ridge and posterolateral marginal tooth. Urosome 3 weakly toothed above base of telson.

Head with raised crown; rostrum strong, attaining end of antennal peduncular segment 1; anterior head lobe acute. Pigmented eyes very large, subrhomboidal, nearly meeting mid-dorsally. Antenna 1 shorter than 2; peduncular segment 2 shorter than 1, 3 very short; flagellum of about 50 short segments; accessory flagellum, short, rod-like. Antenna 2, peduncular segment 4 stout, margins with numerous plumose and simple setae; peduncle 5, posterior margin with a few plumose setae, anterior margin finely calceolate; flagellum of more than 50 short calceolate segments.

Upper lip rounded below. Lower lip broad, inner lobes weak, fused medially. Mandible, molar large, triturating surface squarish, edges lined with short blades; spine row

with 6-7 slender blades; left lacinia 5-6 dentate, right lacinia bifid; incisor with short cutting edge, toothed distally; palp large, segment 3 longer than 2, narrowing apically. Maxilla 1 inner plate with 2 apical setae; palp slender, acute. Maxilla 2, inner plate very broadly rounding apically, marginal setae short. Maxilliped, palp powerfully raptorial, segments 2 and 3 broadened; outer plate ordinary, inner plate broad, with 16 short apical spines.

Coxal 1 strongly produced anteriorly, tip acute, deflexed. Coxae 2-4 medium, about as deep as wide. Coxa 4 distinctly excavate behind. Gnathopod 2 slightly larger than 1; bases stout, hind margin lined with short spines; carpal lobes medium; propods broadly ovate; palmar margins oblique; dactyl-tip depression at posterior angle large, lined behind and medially with 3-4 groups of short spines, and 3 stouter outer marginal spines.

Peraeopods 3 and 4 stout, margins thickly short-setose; segments 4 and 5 subequal; dactyls regular (about 2/3 length of segment 6). Coxa 5 shallowly aequilobate. Peraeopods 5 and 6 stout, subsimilar in form and size; bases acutely produced posteriorly; segments 4-6, hind margins highly setose; dactyls strong. Peraeopod 7 larger than 5 and 6, basis broad, lower hind lobe acute; segment 4-6 setose behind. dactyl straight.

Pleon plates 2 and 3 wide, deep, hind margins nearly straight; lower and posterior margins of pleon 3 finely serrate. Uropods 1 and 2 elongate, rami narrowly lanceolate, margins serially lined with numerous short spines, outer ramus distinctly the shorter. Uropod 3, rami long, lanceolate, inner margins setose and spinose. Telson elongate, narrow, nearly reaching tip of uropod 3, narrowly cleft about 30% of its length.

Coxal gills large, broad. Brood plates broad, margins strongly simple-setose.

Taxonomic and distributional commentary. Shoemaker (1955) recorded the species from off Pt. Barrow, Alaska, in depths of 35 - 50 m. On the Asiatic coast it occurs southward to the Sea of Japan (Gurjanova, 1951).

The type species, *R. aculeata*, entrains more plesiomorphic characters states than any of the ~50 world-wide species to date. It stands in isolation from its nearest relatives at the 50% similarity level (Fig. 34, p. 51).

***Rhachotropis gubilata* J. L. Barnard**
(Fig. 13)

Rhachotropis gubilata J. L. Barnard, 1964: 34, fig. 28. Barnard & Karaman, 1991: 338.

Material Examined: USA: R/V Yaquina, Stn BMT 281, Off Oregon, Cascadia Abyssal Plain (44° 38.55'N, 127° 39.05'W) OSU Dept. Oceanogr., 2816 m, May 19, 1971 - 1 female br. II (slide mt.)

Taxonomic and distributional commentary. This species, originally described from the Panama Basin, evinces a number of plesiomorphic character states, and does not

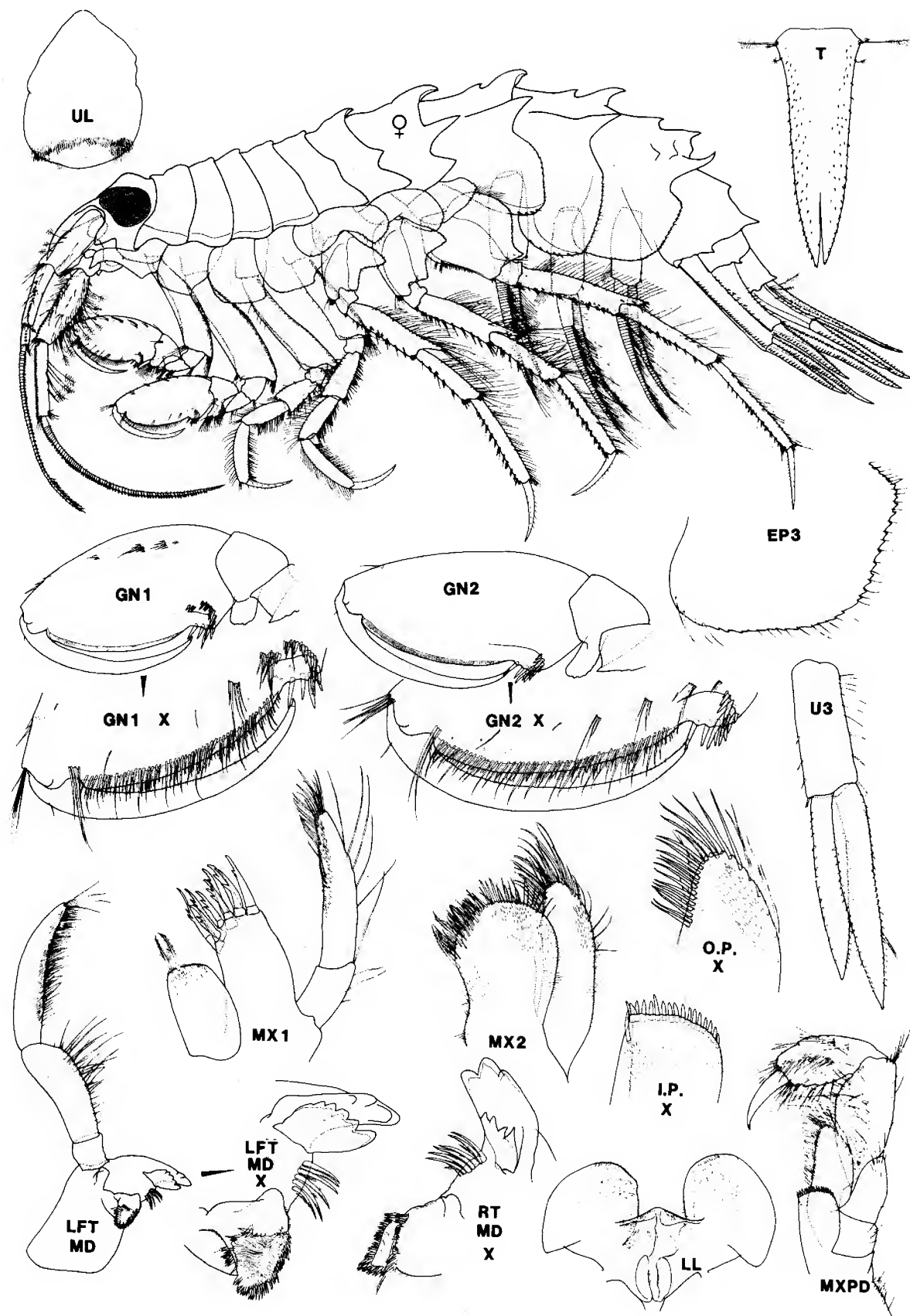


FIG. 12. *Rhachotropis aculeata* (Lepechin) Female ov. (31 mm). Off Wainwright, Alaska.

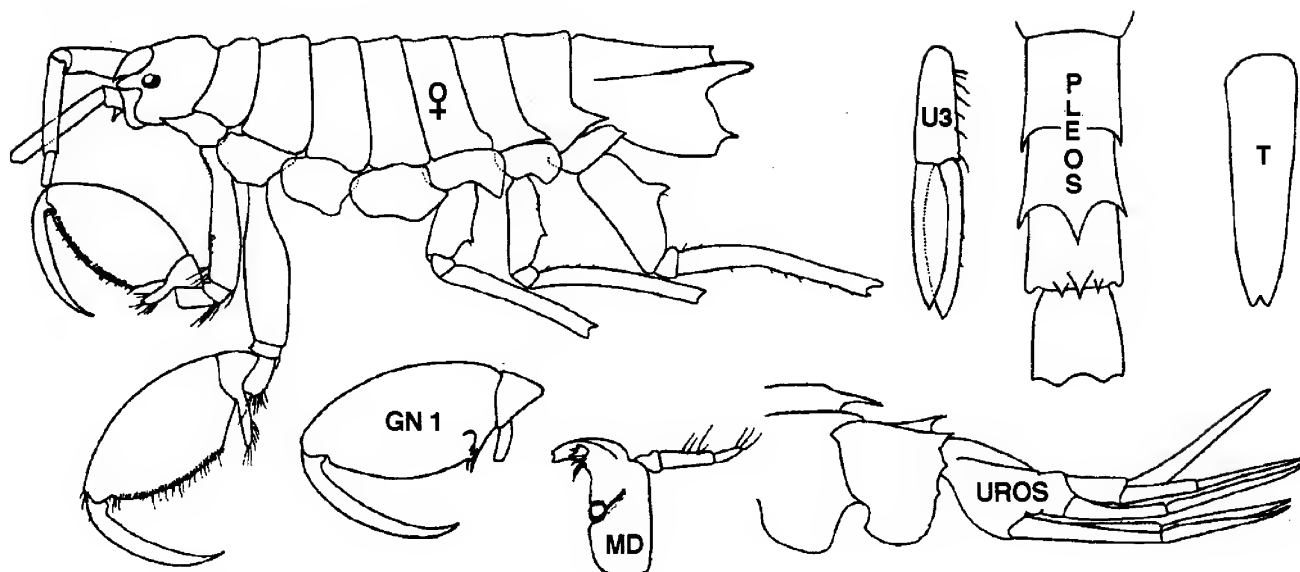


FIG. 13. *Rhachotropis gubilata* Barnard, 1964. Female (17.0 mm). Panama Basin.

compare closely to any of the known N. Pacific deep-water species. The plesiomorphic character states includes the eye remnants, the anteriorly acutely toothed coxa 1, the acutely toothed posterior margins of the bases of pereopods 5-7 (reminiscent of *R. aculeata*?), and the broad rami of uropod 3. Apomorphic character states include the relatively short rostrum, narrower form of the bases of pereopods 5-7, and nearly totally fused telson lobes.

***Rhachotropis helleri* (Boeck)**

(Fig. 14)

Rhachotropis helleri Sars, 1895: 426, pl. 150.—Gurjanova, 1951: 708, fig. 492.—Barnard & Karaman, 1991: 339.

Taxonomic and distributional commentary. This wide-ranging holarctic species is included here because of the records of Gurjanova (loc. cit.) from the Chukchi and Bering Sea regions. The B. C. records of Wailes (1931), Fulton (1968), and Austin (1985) are unconfirmed. *R. helleri* is closely related to *R. macropus* Sars, but less closely similar to the bathyal N. American Pacific species *R. calceolata* n. sp. (below), and *R. boreopacifica*, n. sp. (p. 29).

***Rhachotropis macropus* G. O. Sars**

(Fig. 15)

Rhachotropis macropus G. O. Sars, 1895: 428, pl. 15(1).—Gurjanova, 1951: 709, fig. 493.—Barnard & Karman, 1991: 339.

Taxonomic and fdistributional commentary. Gurjanova (loc. cit.) includes an early record by Derzhavin (1930) from the Sea of Japan. This 16 mm. eyed species occurs in depths of 100-800 m. and may be expected to occur in North American offshore waters of the Chukchi Sea. In its elongate antennal peduncles, strongly produced coxa 1, slender dactylate pereopods 3 and 4, elongate pereopod 7 and subovate gnathopod propods, *R. macropus* resembles

the *boreopacifica* group (p. 29), but the deeply cleft telson may link it more closely to *R. calceolata*, n. sp. (below).

***Rhachotropis calceolata*, new species**

(Fig. 16)

Material Examined: BRITISH COLUMBIA: Queen Charlotte Islands, northwest of Englefield Bay (53°05.08'N, 133°00.08'W to 53°06.58'N, 133°01.22'W), RBCM/CMN Deepwater II Stn. 91-1-11, 0-1227 otter trawl, March 21, 1991. - 1 female (8.7 mm) Holotype (slide mount), CMN-Cat. No. pending.

Diagnosis. Female ov. (8.7 mm): Body medium, compressed. Peraeon segments 1-7 and pleon segment 3 lack dorsal teeth or mucronations. Pleon 1 and urosome 1 with short postero-dorsal tooth; pleon segment 2 with postero-dorsal and dorsolateral mucronations. Rostrum slender, produced; anterior head lobe, apex blunt. Pigmented eyes lacking. Antenna 1, peduncle 1 stout, peduncle 2 slender, subequal; segment 3 medium (1/3 length of segment 2), calceolate; flagellum 14-segmented, proximally calceolate; accessory flagellum very short, subconical. Antenna 2 slightly the longer; peduncular segment 5 slender, longer than segment 4, both calceolate; flagellum ~12-segmented, proximal 5 segments calceolate; calceolate relatively large, receptacle broad, orbicular (tympanic - Barnard, 1967), distal elements forming a short narrow central cone.

Mandible, molar narrowing distally to small grinding surface; spine row with 4-5 blades and accessory setae; left lacinia irregularly 8-9 dentate; right lacinia essentially bifid, 1 cusp bifid; cutting edge of incisor long, nearly smooth; palp segment 3 slender slightly longer than segment 2, apex acuminate. Maxilla 1, inner plate with 2 apical setae, palp slender. Maxilla 2, inner plate broad, inner margin proximally with 2 longer plumose setae. Maxilliped, palp large, powerful, segment 2 somewhat broadened; outer plate broad; inner plate with 4 apical spines.

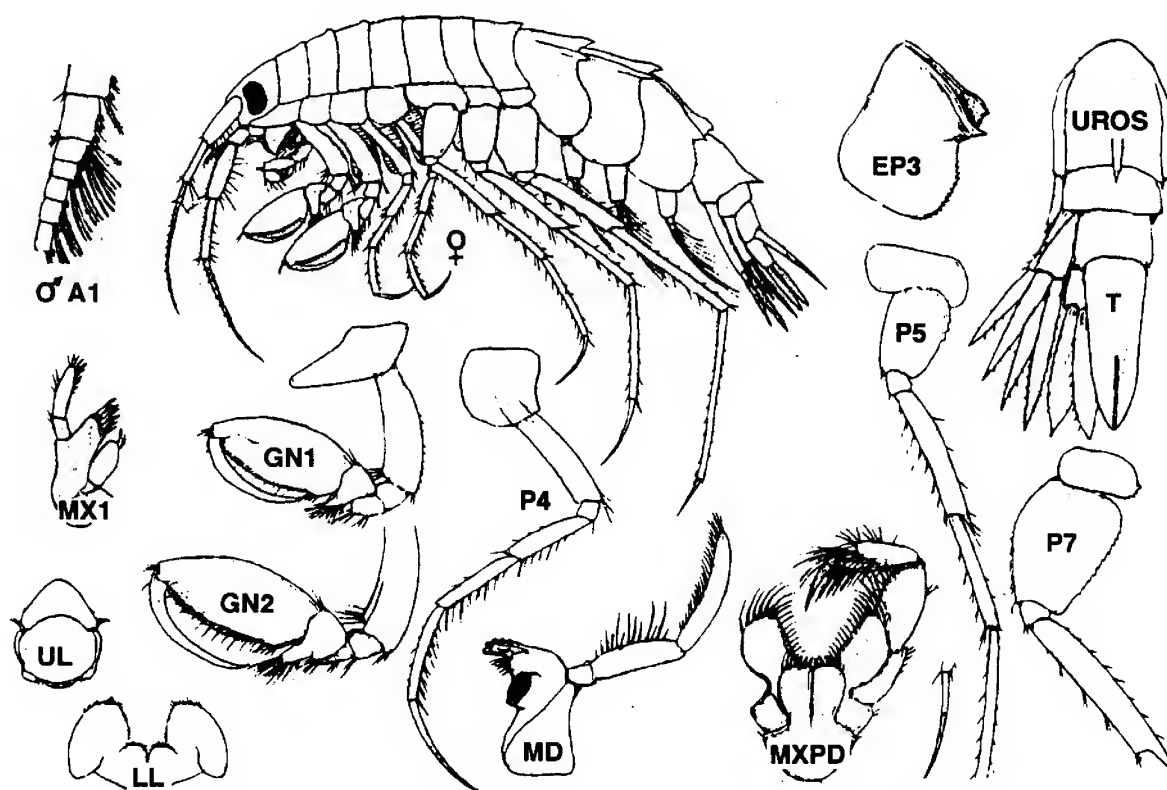


FIG. 14. *Rhachotropis helleri* Boeck Female, Male Norwegian Sea 400 m.
(modified from Sars, 1895)

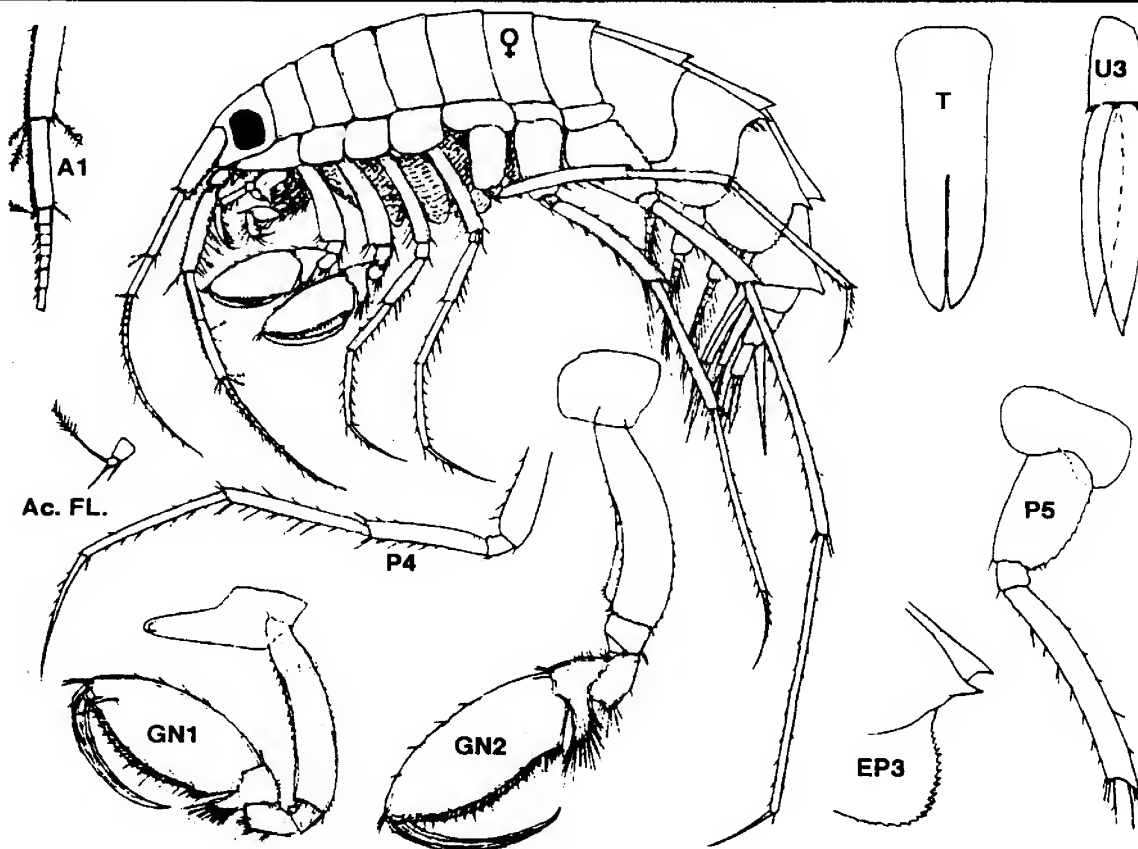


FIG. 15. *Rhachotropis macropus* G. O. Sars, 1895 Female (16.0 mm)
Northeastern Atlantic to Japan Sea, 100 to 800 m. (modified from Sars, 1895)

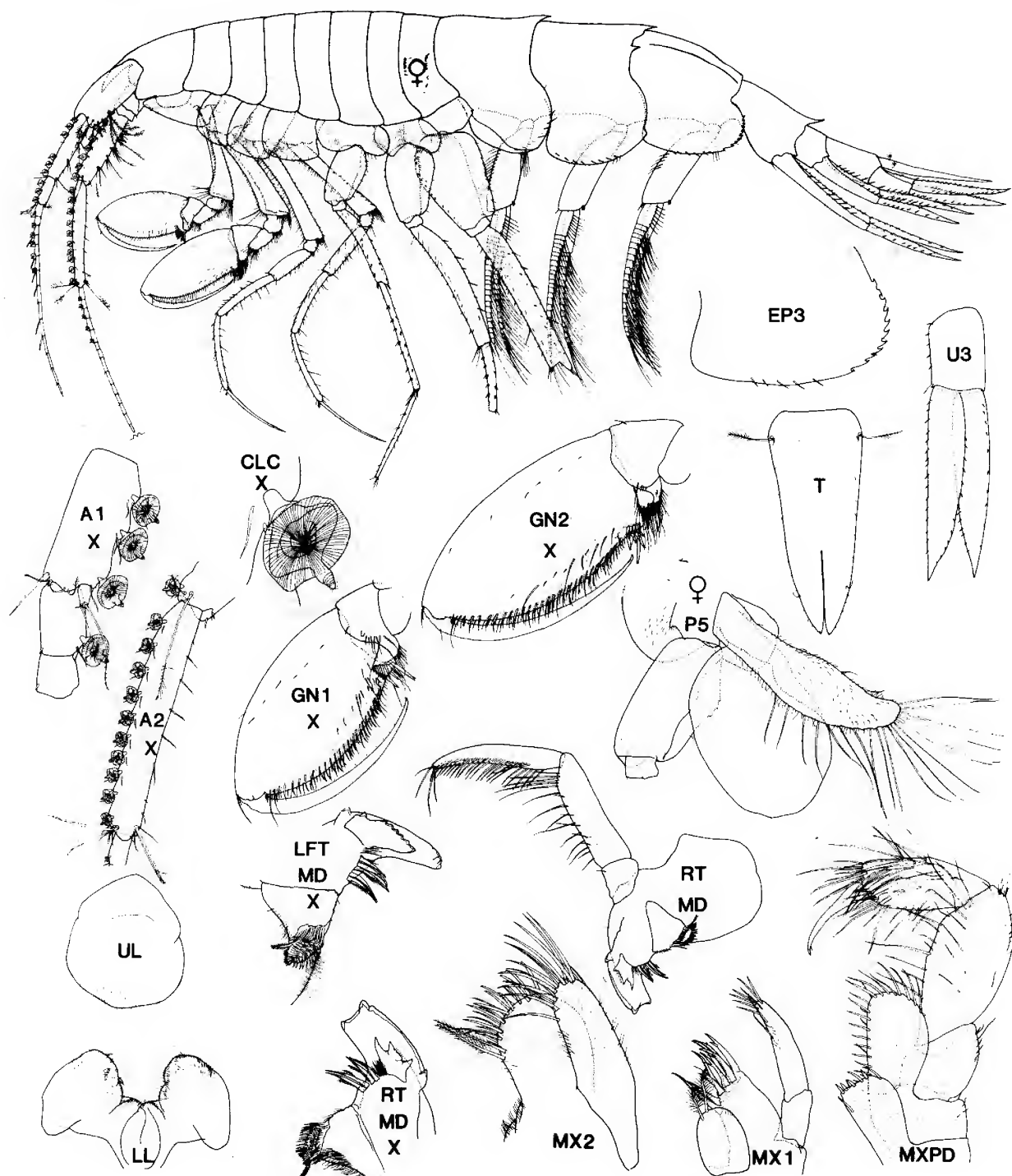


FIG. 16. *Rhachotropis calceolata*, new species. Female (8.7 mm). Northwest of Englefield Bay, Queen Charlotte Islands, B. C., 0-1227 m.

Coxa 1 produced anteriorly, apex subacute; coxae 2-4 wider than deep; coxa 4 shallowly excavate behind. Gnathopod 2 larger than gnathopod 1; bases broadening distally; carpus, posterior lobe relatively short; propods shallowly ovate, hind margin very short, palmar margin very long, postero-distal angle with outer and inner clusters of closing spines.

Peraeopods 3 and 4 slender, segment 4 slightly shorter than 5; dactyls elongate (about = segment 6). Coxae 5 and 6 shallowly anterolobate. Peraeopods 5-7 unequal in form and

size, peraeopod 5 shortest, 7 longest (distal segments missing in type); bases medium broad, narrowing distally, weakly lobate below.

Pleon plates 1-3 broad, lower margins rounded, spinose; hind margin of 3 strongly convex, serrate. Uropods 1 and 2, rami narrowly lanceolate, subequal, not reaching tip of uropod 3. Uropod 3, rami medium broad, subequal, margins finely spinose. Telson medium, narrowing, cleft ~1/3 length, apex not attaining tips of uropod 3.

Coxal gills large, orbicular, smallest on peraeopod 7.

Broods plates broad, narrower and strap-like on pereopod 5, marginal setae long. Male: unknown.

Etymology. The Latin name "calceolata" alludes to the large and conspicuous calceoli of the female antennae

Taxonomic commentary. *Rhachotropis calceolata* is known only from a single specimen at the type locality. Phyletically, it appears most closely related to *R. helleri* (Boeck) and *R. macropus* Sars in its strongly dissimilar pereopods 5-7, strong antennal calceolation, medium deep coxae 1-4, and deeply cleft telson. However, its weak pleonal mucronation, short carpal lobes of the gnathopods, and slender, elongate pereopods 3 and 4 are specifically distinctive.

***Rhachotropis boreopacifica*, new species**
(Fig. 17)

Material Examined: BRITISH COLUMBIA: Off Vancouver I., G. B. Reed Stn. 68-32 (48°21'N 126°08'W) Agassiz trawl, 549 m. - 1 female br. I (10.5 mm), Holotype (slide mount), CMN Acc. No. 68-211. 1 female Paratype. (CMN Cat. Nos. pending).

Diagnosis. Female br I (10.5 mm): Body slender, somewhat elongate. Mid-dorsal mucronations on pereon segments 6 and 7, pleon segments 1-3, and urosome segment 1; dorso-lateral ridge and mucronation on pleon segments 1-3. Rostrum medium, extending beyond sharply rounded head lobe. Pigmented eyes broadly reniform. Antennae slender, sub-equal, finely calceolate on peduncles and proximal flagellar segments. Antenna 1, peduncular segments 1 and 2 subequal, 3 medium (1/3 length of segment 2); flagellum 19-segmented; accessory flagellum minute, with long apical seta. Antenna 2, peduncular segments 4 and 5 slender, hind margins setose, anterior margins calceolate; flagellum 17-segmented.

Mandible, molar large, triturating surface reduced; spine row with 3-4 blades; left lacinia 6-7 dentate, right lacinia appearing trifid; main cutting edge of incisor denticulate; palp stout, segment 3 elongate, narrowing apically. Maxilla 1, inner plate with 2 apical setae; palp ordinary. Maxilla 2, inner plate broad, apical marginal setae not differentiated. Maxilliped, palp strong, segments little broadened; outer plate regular, inner plate with 4-5 apical spines.

Coxa 1 strongly produced anteriorly, apex acute. Coxae 2-4 shallow, broader than deep; coxa 4 weakly excavate behind. Gnathopod 2 slightly larger than 1; bases ordinary. Carpal lobes relatively short and broad; propods subsimilar in form, subovate, hind margin short, palmar margin with large dactyl-tip depression at palmar angle, with 3-4 inner marginal spines (1 elongate), and 3 stout outer marginal spines.

Pereopods 3 and 4 slender; segment 4 slightly shorter than 5; dactyls elongate (~= segment 6). Coxa 5 shallowly aequilobate. Pereopods 5 and 6 slender, subequal; bases narrowing distally, weakly lobate behind; dactyls elongate (> 1/2 segment 6). Pereopod 7 distinctly the longest; basis

narrowing and weakly lobate distally; dactyl slender, straight.

Pleon plates 1 and 2 rounded below, nearly straight behind; pleon plate 3 nearly straight below, strongly convex and serrated behind. Uropods 1 and 2 very long, rami extending to tip of uropod 3; uropod 2, outer ramus distinctly shorter than inner ramus. Uropod 3, rami medium, lanceolate, subequal, inner margin of inner ramus weakly setose. Telson very long, slender, reaching nearly to tip of uropod 3, basally with elongate lateral plumose setae, apex shallowly cleft. Coxal gills plate-like, not pleated

Etymology: The species name alludes to its known occurrence in the North Pacific marine region.

Taxonomic and distributional commentary. *Rhachotropis boreopacifica* is known only from the type locality. Its general affinities are with *R. helleri* (Boeck) and *R. macropus* G. O. Sars, circumpolar species that have been recorded previously from the Bering and Chukchi Sea regions of the western North Pacific (Gurjanova, 1951). However, it appears similar in many points of detail to *R. barnardi*, new species, from the Oregon coast, as detailed below.

***Rhachotropis barnardi*, new species**
(Fig. 18)

Rhachotropis clemens J. L. Barnard, 1971: 10, figs 6, 7 (eyed material). (Selection of type specimen pending).

Material Examined. BRITISH COLUMBIA: 34 specimens in 15 lots at 10 stations, as follows: Off Queen's Beach, Jervis Inlet, ELB Stn. J1, 350 m. dredge, May 12, 1977 - 4 females, 2 males (slide mounts); Burrard Inlet and offing, Nov. 2-3, 1977: ELB Stns. P4 (6 females); P6 (1 female); P7 (1 female (slide mount), 3 males); P8 (5 females, 1 male). Burrard Inlet and offing, July 5, 1978: ELB Stns. V5, 150 m. dredge - 1 male; V6, 150 m. nat. dredge - 4 females, 3 males (slide mounts). Off Hammond Beach, Departure Bay, ELB Stn. B1, 17.5 m. nat. dredge, May 14, 1977 - 1 male. Nukumis Bay, Vancouver I., B. C., PF and MB colls. - 1 female. English Bay, B. C., N McD coll., 1977 - 1 female.

Diagnosis. Male (3.3 mm) (amplifies significant features not fully treated in the original description, based on Barnard's original 2 lots from off the coast of Oregon):

Body mid-dorsally smooth on pereon, mid-dorsally and dorso-laterally ridged and mucronate on pleon segments 1 and 2, dorso-laterally ridged on pleon 3, and strongly toothed mid-dorsally on urosome 1, and laterally above base of uropod 1. Rostrum strong, apex acute, not deflexed; anterior head lobe blunt, almost rounded. Eye broadly sub-reniform, consisting of a loose aggregation of 40-50 weakly pigmented facets. Antenna 1, peduncle 1 with strong distomedial cusp (both sexes). Antennae calceolate in female.

Mouthparts not treated by Barnard (1971), but relatively plesiomorphic in B. C. material, as in *R. boreopacifica*.

Coxae 1-4 shallow, little deeper than wide; coxa 1 produced, broadly rounded, hind corner with small notch and

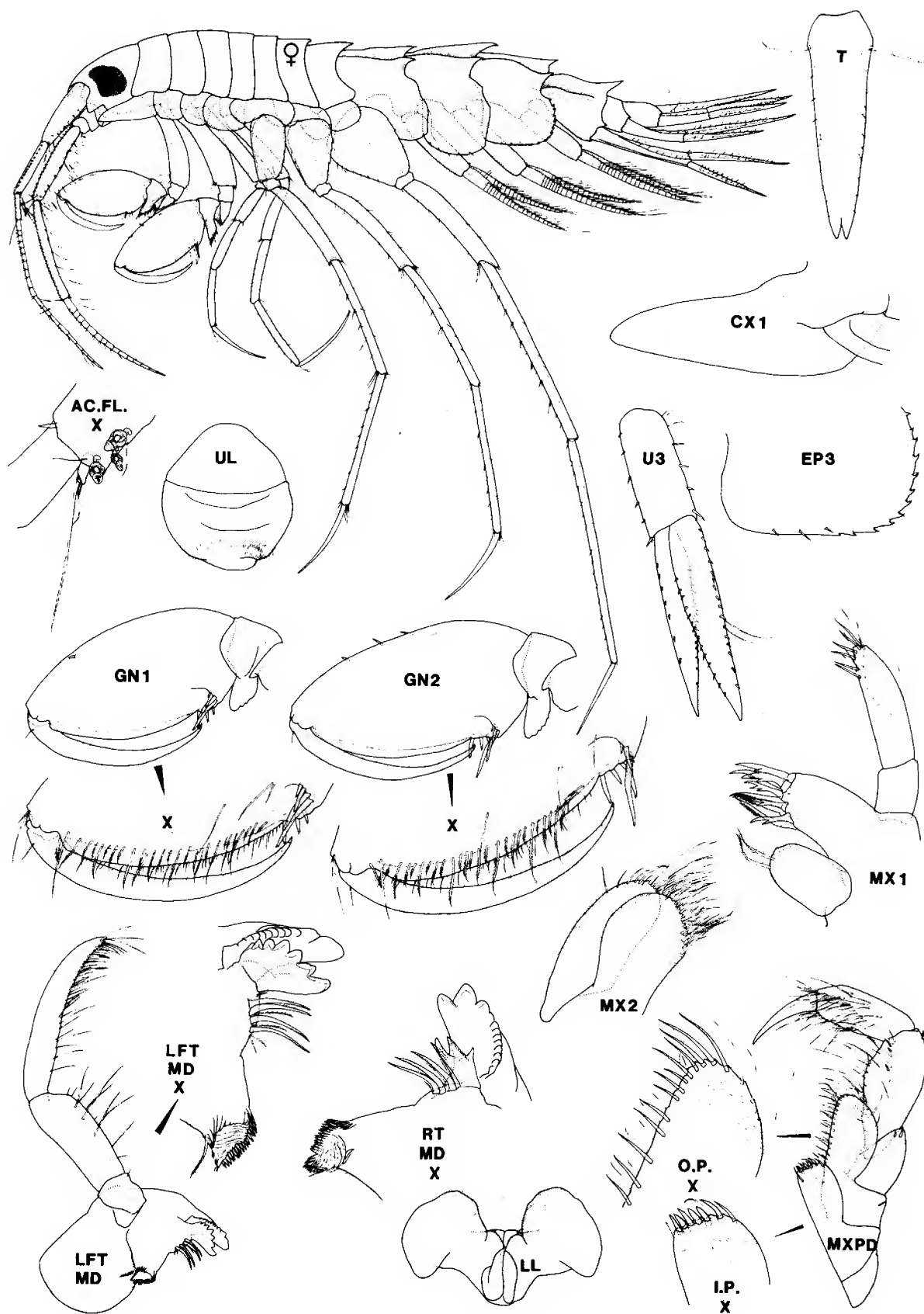


Fig. 17. *Rhachotropis boreopacifica*, n. sp. Female br. I (10.5 mm). Off Vancouver I., B. C., 549 m.

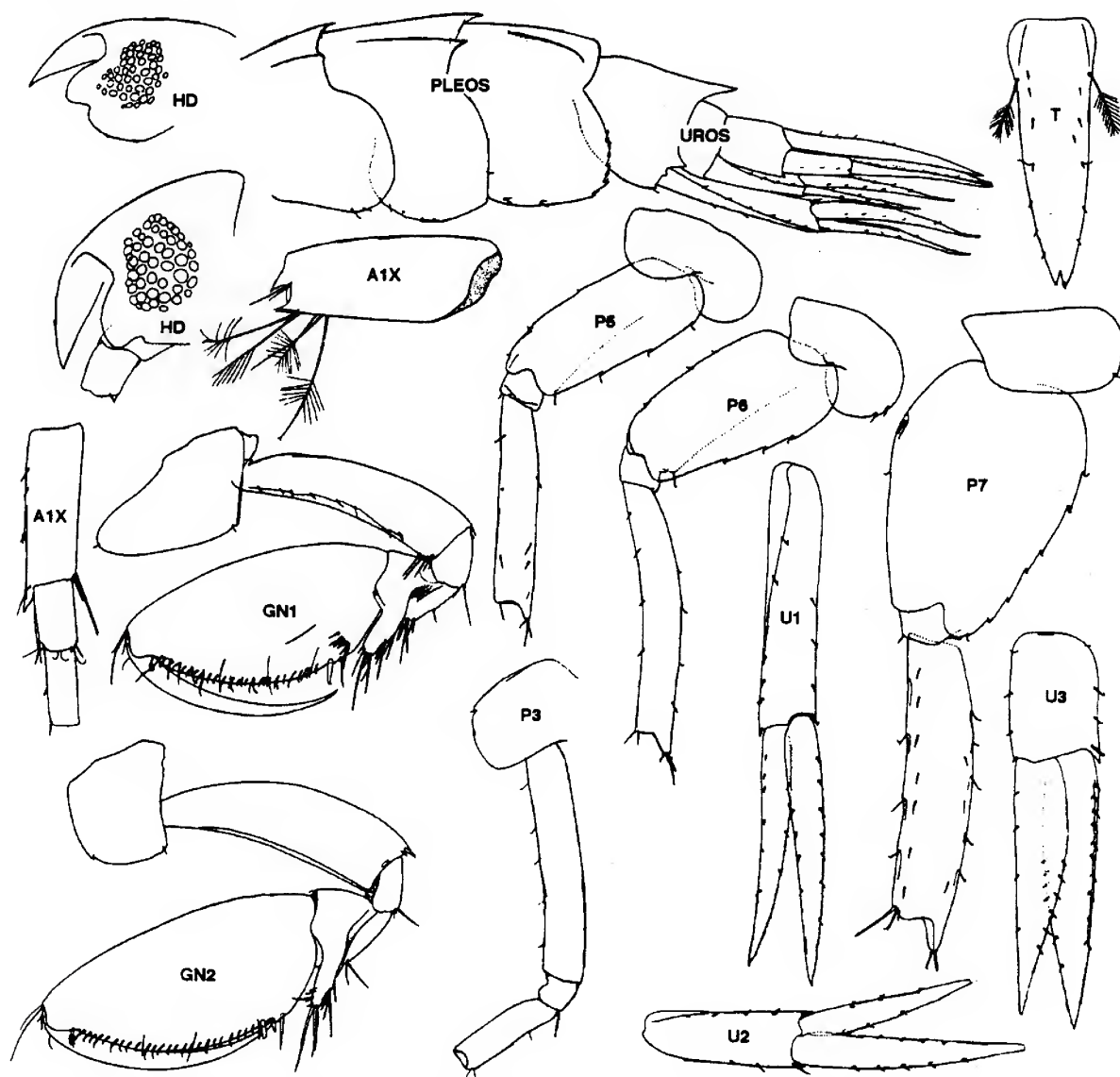


FIG. 18. *Rhachotropis barnardi* new species. Male (3.3 mm).
(modified from Barnard, 1971). Off Oregon, 200 m.

seta. Gnathopods 1 and 2, propods subovate, closely similar in size and form; carpal lobes narrow, 2 the longer, apices with 2-3 slender spines; palmar margins with few long setae; posterior angle with 2 outer marginal spines at dactyl tip depression.

Peraeopods 3 and 4 slender, segment 4 short (dactyls missing, presumably slender). Peraeopods 5-6, coxae postero-lobate; bases medium, narrowing distally, lobate below. Peraeopod 7 stouter and longer than 5 and 6; basis convex and weakly serrate behind, narrowing distally, lobate below. Pleon plate 2, hind corner weakly obtuse; pleon plate 3, hind corner rounded, lower hind margin irregularly serrate. Uropod 1, rami narrow, elongate, subequal, tips extending to tips of uropod 3. Uropod 3, rami subequal, margins spinose. Telson elongate, length > 3X basal width, basally with pair of large lateral plumose setae; apex sharply notched, nearly attaining tips of rami of uropod 3.

Coxal gills and brood plates not described.

Etymology. The species is named in honour of the late J. L. Barnard who first described and figured the Oregon material.

Taxonomic and distributional commentary. Barnard (loc. cit.) concluded that this form was an eyed variant of *R. clemens*, a bathyal species that he had earlier described from the Cedros Trench (p. 32). However, as noted in the key, and above, several external features of *R. barnardi* differ specifically from those of *R. clemens*, and some are closer to those of *R. boreopacifica* (above). These include not only the pigmented eyes, but the more elongate propod, stronger carpal lobe, and less spinose basis of gnathopod 1; the broader and distinctly more lobate bases of peraeopods 5-7, the more rounded pleon plate 3, the broader rami of uropods 1-3, the more elongate telson, and lack of dorso-lateral mucronation on pleon 3. The last feature, long sharply acute rostrum, and asetose rami of uropod 3 readily separate *R. barnardi* from *R. boreopacifica*.

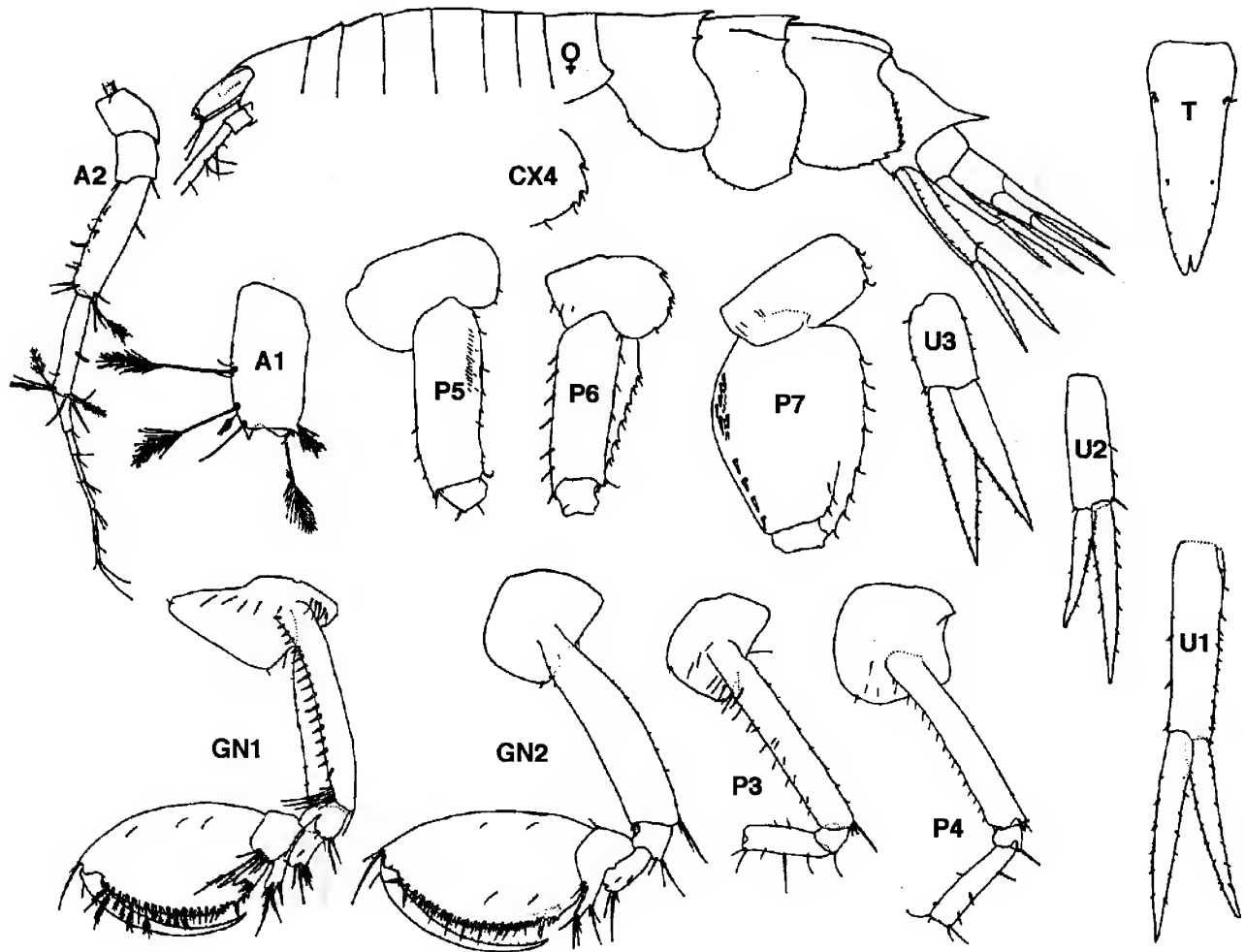


FIG. 19. *Rhachotropis clemens* Barnard, 1967. Female (4.5 mm)
Off S. California, ~800 m. (modified from Barnard, 1967)

Rhachotropis clemens J. L. Barnard
(Figs. 19)

Rhachotropis clemens J. L. Barnard, 1967: 16, fig. 5.—J. L. Barnard, 1971: 10, figs. 6, 7.

Taxonomic and distributional commentary. The original description of this species (Barnard, 1967a) was based on anoculate material (female- 4.5 mm) from depths of 791-842 m. in the Cedros Trench, off Baja California. Barnard did not include details of the mouthparts, coxal gills, and brood plates, character states of which are proving phylogenetically significant. Description of these features would require re-examination of the 3 specimens from the type locality, not performed in the present study.

However, in comparing *R. clemens* with other N. American Pacific species, the overall form of its pereopods 3-7, uropods and telson, and mucronate urosome 1, would relate it more closely to the northern sublittoral eyed species, *R. barnardi* and *R. boreopacifica* than to other bathyal species of the Cedros Trench, or to the sublittoral eyed *R. luculenta*

of the Gulf of California.

The smaller Oregon material to which Barnard referred this name (1971, and p. 29) has generally fewer spines, the telson is relatively longer and its apex is less deeply notched than in the larger Californian specimens. Such differences between sizes and between male and female specimens of the same species would not be unexpected. However, transcending differences in sex and size, *R. clemens* is distinctive not only in its total lack of pigmented eyes, but also in its short anterior head lobe, relatively short antennae 1 and 2, the strong plumose setal armature of antennal ped-uncular segments, the deep gnathopod propods with relatively strongly setose palmar margins, the narrow, nearly alobate bases of pereopods 5 and 6, the squarish hind corner of pleon plate 3, the short, slender uropod rami, the relatively short telson (length <3X basal width), with asymmetrical apical lobes of which do not nearly attain the tips of uropod 3. In some features (e.g., form of antennae and gnathopods), *R. clemens* somewhat resembles the northern sublittoral species complex of *R. inflata* (G. O. Sars), *R. minuta*, and *R. conlanae*, but differs significantly otherwise.

***Rhachotropis oculata* (Hansen)**
(Fig. 20)

Tritropis oculata H. J. Hansen 1888: 140.

Rhachotropis oculata G. O. Sars 1895: 424, pl. 153.—Stebbing, 1906:350.—Gurjanova, 1951: 712, fig 496.—Bousfield, 1973: 78, pl. XI.—Austin, 1985: 590.—Staude, 1987: 378.

Material Examined. BRITISH COLUMBIA: 125 specimens, in 15 lots, mainly from the north central coast of British Columbia, south to Burrard Inlet:

ELB Stn. H37, Open Bight, mouth of Rivers Inlet, 50-60 m. dredge, fine sand and shell, July 22, 1964. - 1 female ov. (10.1 mm), (slide mount). Off Spanish Banks, Burrard Inlet, Stn. EB7, muddy sand, 26 m. dredge, June 16, 1976 - 2 imm. specimens; West Bay, 3/4 mile south, ELB Stn. P3, 30 m. dredge, Nov. 2, 1977 - 1 female, 1 imm. Trevor Channel, off Brady's Beach, V. I., ELB Stn. B13, 6-24 m dredge, May 25, 1977 - 1 male.

Diagnosis. Female ov. (10.1 mm): Body medium broadest in peraeon. Peraeon segment 7 and pleon segments 1-3 with postero-dorsal mucronation, very short and deflexed on 3; pleon segments 1-3 each with dorso-lateral ridge and tooth. Urosome segment 1 lacking dorsal process. Rostrum medium, exceeding short acute lateral head lobe. Pigmented eyes large, rhomboidal, nearly meeting mid-dorsally. Antenna 1, peduncular segment 1 and 2 stout, 2 short, 3 very short; flagellum 20-segmented, weakly calceolate; accessory flagellum rod-like, 1-segmented. Antenna 2 slightly longer than 1; peduncular segment 4 strongly setose behind, segment 5 more strongly calceolate anteriorly; flagellum calceolate, 25-segmented.

Mandible, molar large, conical, grinding surface large; spine row with 3-4 narrow blades; left lacinia 6-dentate; right lacinia trifid; incisor, cutting margin relatively short; palp stout, segment 3 slender, distinctly longer than segment 2, narrowing distally. Maxilla 1, inner plate with 2 apical setae, palp stout. Maxilla 2, inner plate shorter and broader than outer, inner margin proximally with single stout plumose seta. Maxilliped, palp strong, segment 2 broadened; outer plate tall; inner plate with 7 apical short spines.

Coxa 1 produced anteriorly, apex sharply rounded; coxae 2-4 shallow broader than deep; coxa 4 weakly excavate behind. Gnathopod 2 larger than 1; bases, anterior and posterior margins lined with short spines; carpal lobes narrow, not strongly produced; propods subsimilar, regularly ovate; hind margin medium; palmar margin with large dactyl-tip depression lined by interior cluster of 4-6 spines (1 elongate), and short outer row of 3 spines.

Peraeopods 3 and 4 medium, strong, segment 4 shorter than 5; dactyls strong (length ~ segment 6). Coxae 5 and 6 shallow, nearly aequilobate. Peraeopods 5 and 6 subsimilar in form and size; bases short, broad, weakly lobate below; hind margins of segments 4-6 of peraeopod 6 bearing spines and setae; dactyls elongate. Peraeopod 7 more elongate;

basis broad, hind lobe acute below; distal segments spinose and weakly setose; dactyl sublinear.

Pleon plate 2, hind corner squarish, slightly acuminate; pleon plate 3, hind margin convex, strongly serrated. Uropods 1 and 2, rami narrow lanceolate, margins strongly serially spinose; uropod 2, outer ramus distinctly shorter than inner ramus. Uropod 3, rami broadly lanceolate, subequal, inner margins setose and spinose. Telson basally broad, medium long, not reaching tip of uropod 3, cleft 40% of its length.

Coxal plates large, subovate.

Taxonomic and distributional commentary. The present material differs little from that described and figured from the North Atlantic coast by the senior author (Bousfield 1973). *Rhachotropis oculata* is amphiboreal and subarctic, ranging southward on both sides of the North Atlantic and North Pacific oceans. On the coast of British Columbia, it is the shallowest ranging species, taken mainly at depths of less than 100 m.

***Rhachotropis inflata* (G. O. Sars)**
(Fig. 21)

Tritropis inflata G. O. Sars, 1882.

Rhachotropis inflata Sars, 1895: 430, pl. 152.—Waiiles, 1931: 41.—Gurjanova, 1951: 713, fig. 497.—Fulton, 1968: 107.—J.L. Barnard, 1971: 12.—Austin, 1985: 590.—Barnard & Karaman, 1991: 338.

Taxonomic and distributional commentary. This relatively small species (female to 8.0 mm) has been well described and figured by Sars (loc. cit) on the basis of material taken at depths to ~100 m. in Norwegian coastal fiords. Although Gurjanova (1951) lists this species from the Bering Sea and Sea of Japan, it was not identified in material of the present North American Pacific study region.

The species is recorded, but not authentically, from the B. C. coast by Waiiles (1931) and Fulton (1968), and from off the coast of Oregon by Barnard (1971), records repeated by Austin (loc. cit). However, its moderately close similarity to *R. conlanae*, and to lesser extent to *R. minuta*, both newly described herein, indicates that a re-examination of the earlier materials is advisable, if possible. *R. inflata* is similar to both *R. minuta* and *R. conlanae* in lacking a dorsal tooth on pleon 3 and urosome 1, in the short antennae, relatively short, weak peraeopods 3 and 4, and the relatively short deeply cleft telson.

However, *R. inflata* differs from both in the relatively slender form of the propod of gnathopod 2, and more uniform length of the palmar setae. Although *R. inflata* is similar to *R. minuta* in having distinct dorso-lateral ridges and mucronations on pleon segments 1-3, it differs further from *R. minuta* in lacking a dorsal tooth on peraeon 7, in its broader less reniform eye, and in its broader and more posteriorly convex basis of peraeopod 7.

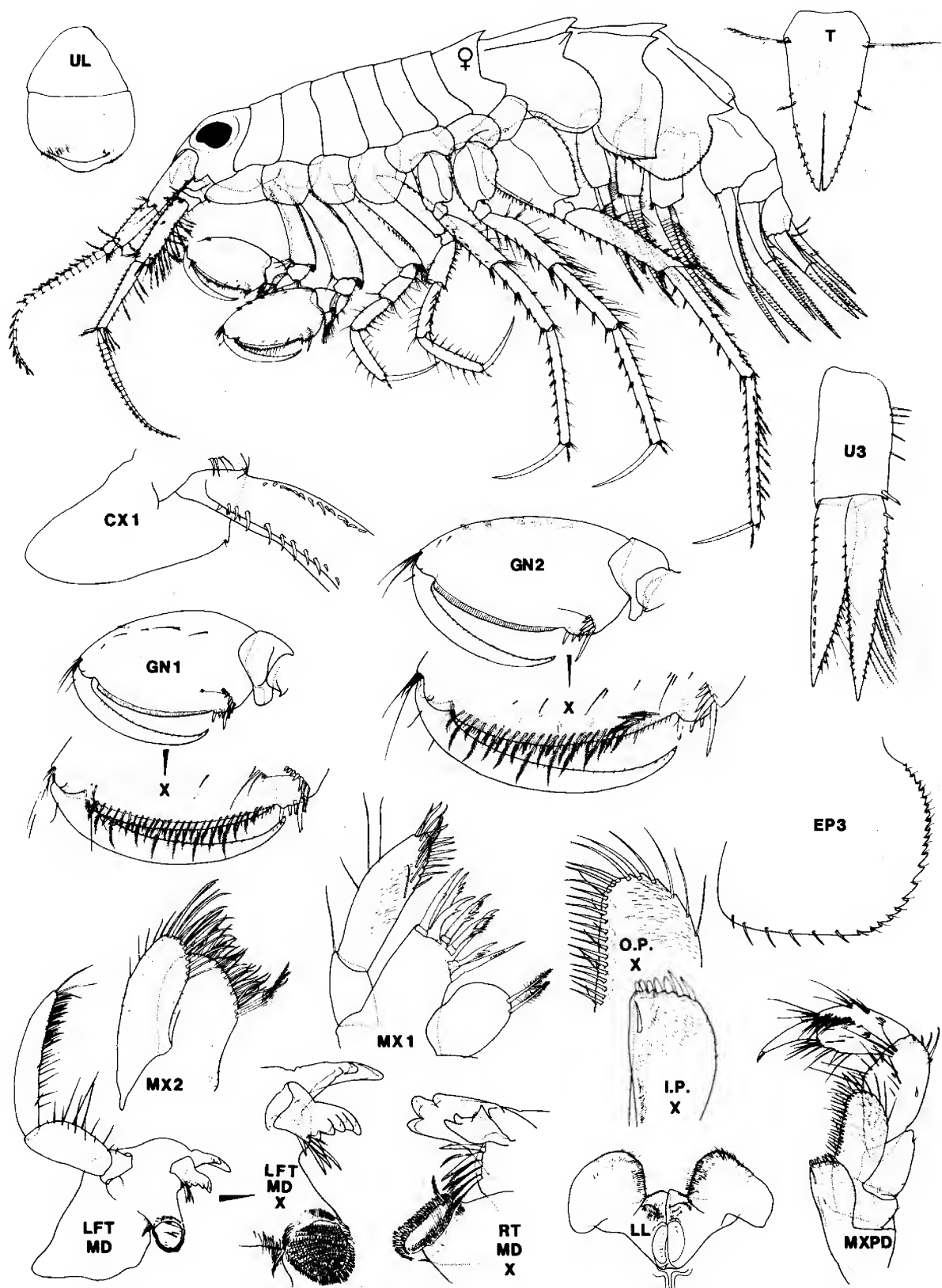


FIG. 20. *Rhachotropis oculata* (Hansen). Female ov. (10.1 mm). Open Bight, B. C., 50-60 m.

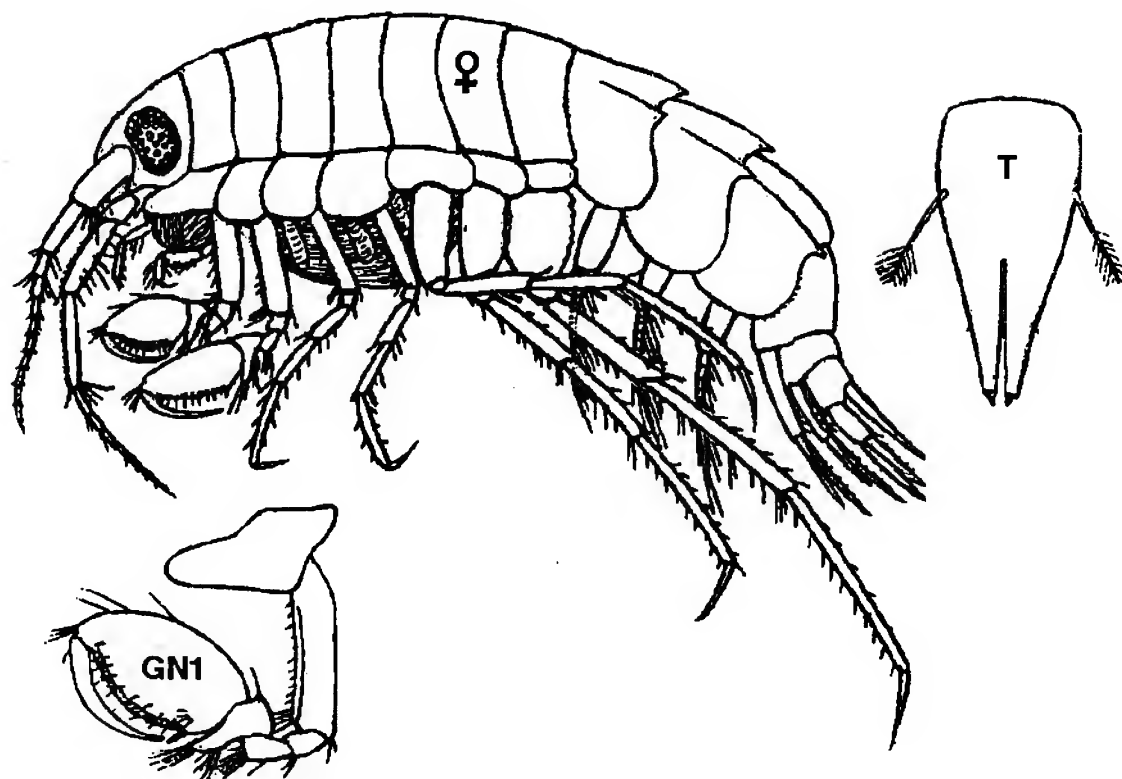


FIG. 21. *Rhachotropis inflata* (G. O. Sars, 1883). Female (8.0 mm)
Off Norway, 200 m. (modified from Sars, 1895)

Rhachotropis minuta, new species
(Fig. 22)

Material Examined: BRITISH COLUMBIA: ELB Stn. P3, West Bay, 3/4 miles south, 60 m. dredge, Nov. 2, 1977 - 1 female ov (3.8 mm) Holotype (slide mount), 2 other female, Paratypes (slide mount), CMN Acc. No. 1977-327.

Diagnosis. Female (3.8 mm): Body small, slender. Peraeon segment 7 with small dorsal and dorso-lateral teeth. Pleon segments 1 and 2 toothed dorsally and dorso-laterally, but pleon segment 3 very weakly so. Urosome 1 with very weak posterior marginal cusps and tooth above junction of uropod 1. Rostrum medium; lateral head lobe short, acute. Eye large, broadly reniform. Antenna 1, peduncular segments short, flagellum 7-segment, not calceolate; accessory flagellum minute, with strong apical spine. Antenna 2, peduncular segments 4 and 5 subequal, 4 setose behind, 5 calceolate anteriorly; flagellum 6-segmented, calceolate basally.

Mandible, molar conical, grinding surface small, surrounded by blade spines; spine row with 3-4 blades; left lacinia 6-dentate; incisor main cutting edge nearly smooth; palp stout, segment 3 longer than 2. Maxilla 1, inner plate with 2 apical setae; palp slender. Maxilla 2, inner plate little broadened, with stout inner marginal seta. Maxilliped ordinary; outer plate not broadened; inner plate with 3 apical spines.

Coxa 1 very strongly produced anteriorly, apex sharply rounded.; coxae 2-4 shallow, wider than deep, coxa 4 shallowly excavate behind. Gnathopod 2 distinctly larger than gnathopod 1; bases with antero-distal cluster of setae; carpus narrowly lobate; propod medium, ovate, posterior angle with inner marginal group of 2 spines and a single stout outer marginal spine; palmar setae longest near hinge.

Peraeopods 3 and 4 ordinary; segment 4 little shorter than 5, dactyls medium (~50% length of segment 6). Peraeopods 5-7 regular 7 distinctly longest; bases of 5 and 6 narrowly lobate, of 7 broader and more strongly lobate below; dactyls regular.

Pleon plate 2, hind corner acuminate; pleon plate 3 strongly rounded and strongly serrated behind. Uropods 1 & 2, rami slender, uropod 2 extending beyond uropod 3. Uropod 3, rami narrowly lanceolate, subequal, margins sparsely spinose. Telson short, extending little beyond peduncle of uropod 3; cleft about 40% of its length, apices spreading slightly.

Coxal gills plate-like, unpleated.

Etymology. From the Latin "minuta" referring to the very small size of the adult animal.

Taxonomic and distributional commentary. *Rhachotropis minuta* is closely similar to *R. conlanae*, n. sp. but differs in the stronger dorsal armature of the pleon, and the normal dactyls. Both species are closest in form to *R. inflata*, (Sars) and to lesser extent to *R. oculata* (Hansen).

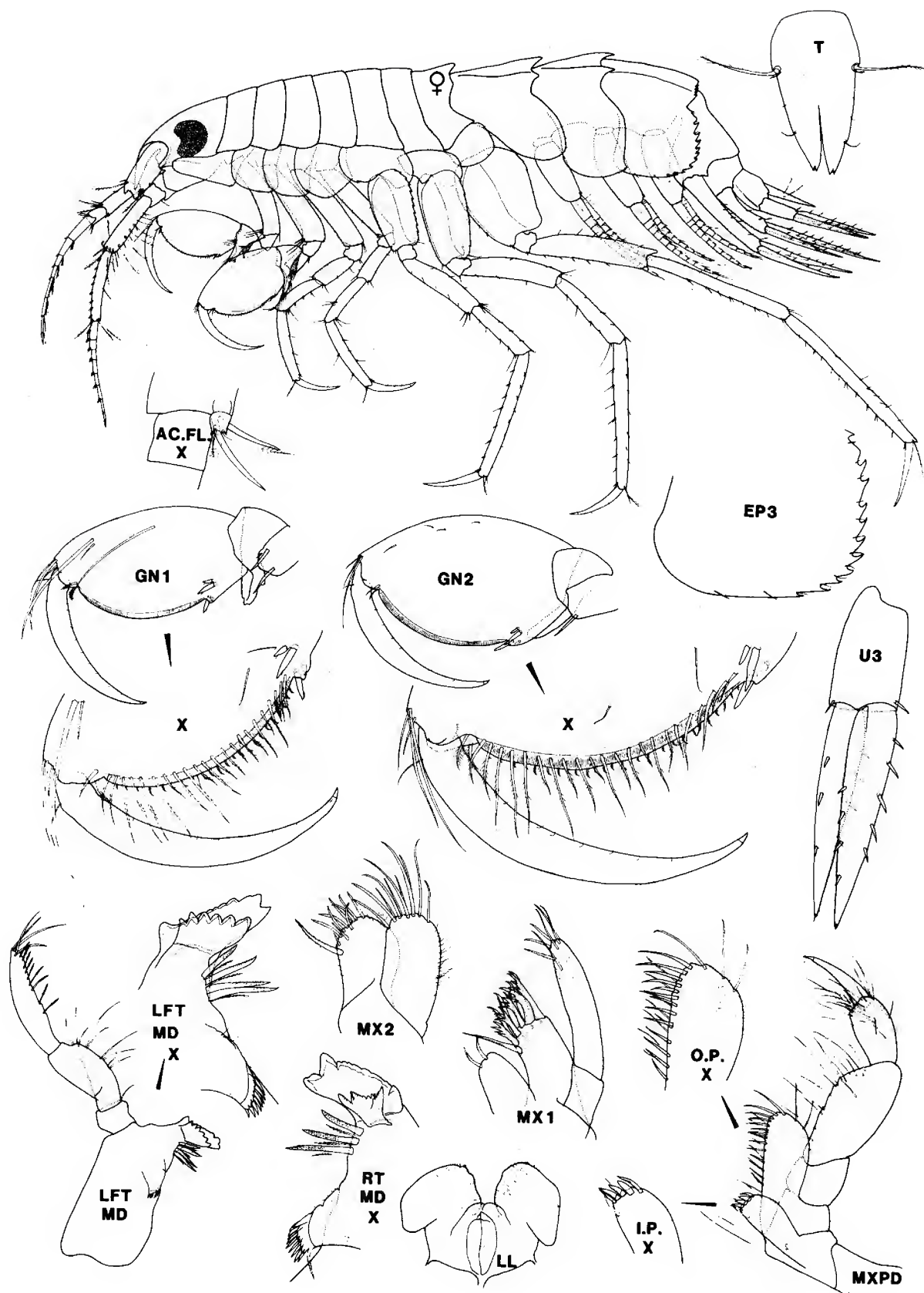


FIG. 22. *Rhachotropis minuta*, n. sp. Female ov. (3.8 mm). West Bay, B. C. 60 m. dredge.

***Rhachotropis conlanae*, new species**
(Fig. 23)

Rhachotropis inflata Austin, 1985, partim?

Material Examined: S.E. ALASKA: Boca de Quadra, across from Bactrian Point (55° 07.9'N, 130° 43.5'W.), 29 m. dive, in sponge bed, K. E. Conlan Stn. 89-2-45, June 27, 1989 - 1 female ov (4.5 mm) Holotype (slide mount); female (4.1 mm) Paratype; about 100 other specimens (no mature males), CMN Acc. No IZ1989-066.

Diagnosis. Female ov. (4.5 mm): Body small, compressed. Peraeon pleon 3 and urosome dorsally unarmed. Pleon 1 with small mid-dorsal cusp, and pleon 2 with very short mid-dorsal and dorso-lateral mucronations. Rostrum medium; anterior head lobe short, acute. Eye very large, round. Antenna 1, peduncular segments short; flagellum 6-7 segmented, lacking calceoli; accessory flagellum very short, apex with stout spine and plumose seta. Antenna 2, peduncular segment 5 longer than 4, both anteriorly marginally calceolate; flagellum calceolate, 7-8 segmented.

Mandible molar columnar, triturating surface small; spine row with 3-4 blades and accessory setae; left lacinia 7-dentate; incisor multidentate; palp stout, segment 3 slightly longer than segment 2. Maxilla 1 inner plate with 1 apical seta; palp large. Maxilla 2, inner plate little expanded, shorter than outer plate. Maxilliped regular; outer plate relatively narrow, inner plate with 4-5 apical spines.

Coxa 1 strongly produced anteriorly, apex subacute. Coxae 2-4 broader than deep, 4 scarcely excavate behind. Gnathopod 2 slightly larger than gnathopod 1; bases, with cluster of antero-distal setae; carpus narrowly produced; propods deeply ovate; posterior angle with a medial group of 3 short spines and a single exterior stout spine.

Peraeopods 3 and 4, segment 4 slightly shorter than 5; dactyls relatively short, stout, unguis short. Peraeopods 5-7 not elongate, increasing posteriorly; bases medium broad and lobate; dactyls short, thick, as in peraeopods 3 and 4.

Pleon plate 2, hind corner acuminate; pleon plate 3 rounded behind with about 10 medium strong serrations. Uropods 1 and 2 rami elongate extending to tips of uropod 3. Uropod 3, rami narrowly lanceolate, subequal, margins spinose. Telson relatively short, extending little beyond peduncle of uropod 3, cleft about 40%, apices slightly spreading.

Coxal gills plate-like, unpleated.

Etymology. The species is named in honour of Dr. Kathleen E. Conlan in recognition of her continuing major contributions to knowledge of amphipod crustaceans.

Taxonomic and distributional commentary. The species is closest to *R. inflata*, but differs in the characters of the key (p. 23). *R. conlanae* is remarkably similar to *R. luculenta* Barnard from sublittoral depths of the Gulf of California. However, it is unique among species of the N. American Pacific coast in its relatively short peraeopods 3 and 4, and short stout dactyls of peraeopods 3-7.

***Rhachotropis luculenta* Barnard**
(Fig. 24)

Rhachotropis luculenta J. L. Barnard, 1969c: 203, Fig. 16.

Taxonomic and distributional commentary. Barnard (loc. cit.) described this small, eyed, calceolate species (male - 4.6 mm) from Bahia de Los Angeles, Gulf of California, at depths of 38-46 m. He compared it most closely with *R. inflata* Sars but noted differences in the dorsal pleon mucronation, rostral shape, length of peraeopod dactyls, and other features. He also compared it with *R. oculata* (Hansen) but noted a greater range of differences in dorsal mucronation and peraeopod features.

R. luculenta differs from all other known eyed species of the northern hemisphere that lack a tooth on urosome 1, including the Mediterranean region, in the combination of the very short flagellum of antenna 1, the very different size and form of the propods of gnathopods 1 and 2, the short segment 4 of peraeopod 3, the double- or triple-toothed posterior margins of the bases of peraeopods 5 and 6, and the much smaller eyes of the female. Regretably, of the mouthparts, only the mandibular palp was figured and mentioned briefly in Barnard's text. In the present study, the balance of character states was found to be relatively advanced (Fig. 34) and least different from the bathyal species, *R. ludificor*, that Barnard described earlier (1967) from bathyal depths of the outer coast of Baja California (see below). *R. luculenta* may be a warm-water species that is unlikely to be found north of Pt. Conception on the N. American Pacific coast.

***Rhachotropis ludificor* Barnard**
(Fig. 25)

Rhachotropis ludificor J. L. Barnard, 1967: 18, fig. 6.

Taxonomic and distributional commentary. The species is based on a male specimen (4.5 mm) taken at a depth of 1720-1748 m in Cedros Trench, Baja California. Barnard (loc. cit.) had readily distinguished it from all eyeless world species described at that time but linked it most closely with *R. distincta* Holmes (1908). *R. ludificor* is here grouped with the eyed, calceolate species *R. luculenta* and *R. conlanae* in sharing the following features: medium strong rostrum; weakly mucronate pleon; dorsal mucronation on urosome 1 minute or lacking; coxa 1 strongly produced anteriorly, with broadly rounded apex; large deep gnathopod propods; lobate bases of peraeopods 5-7; non-setose margins of uropod 3 rami, and relatively short, deeply cleft telson. *R. ludificor* more closely resembles *R. luculenta* in the slender distal segments and dactyls of peraeopods 3 and 4 and triple micro-cusping of the postero-dorsal margin of pleon segment 3. It differs, however, in the more elongate antennal peduncular segments, apparent lack of antennal calceoli, and total lack of pigmented eyes.

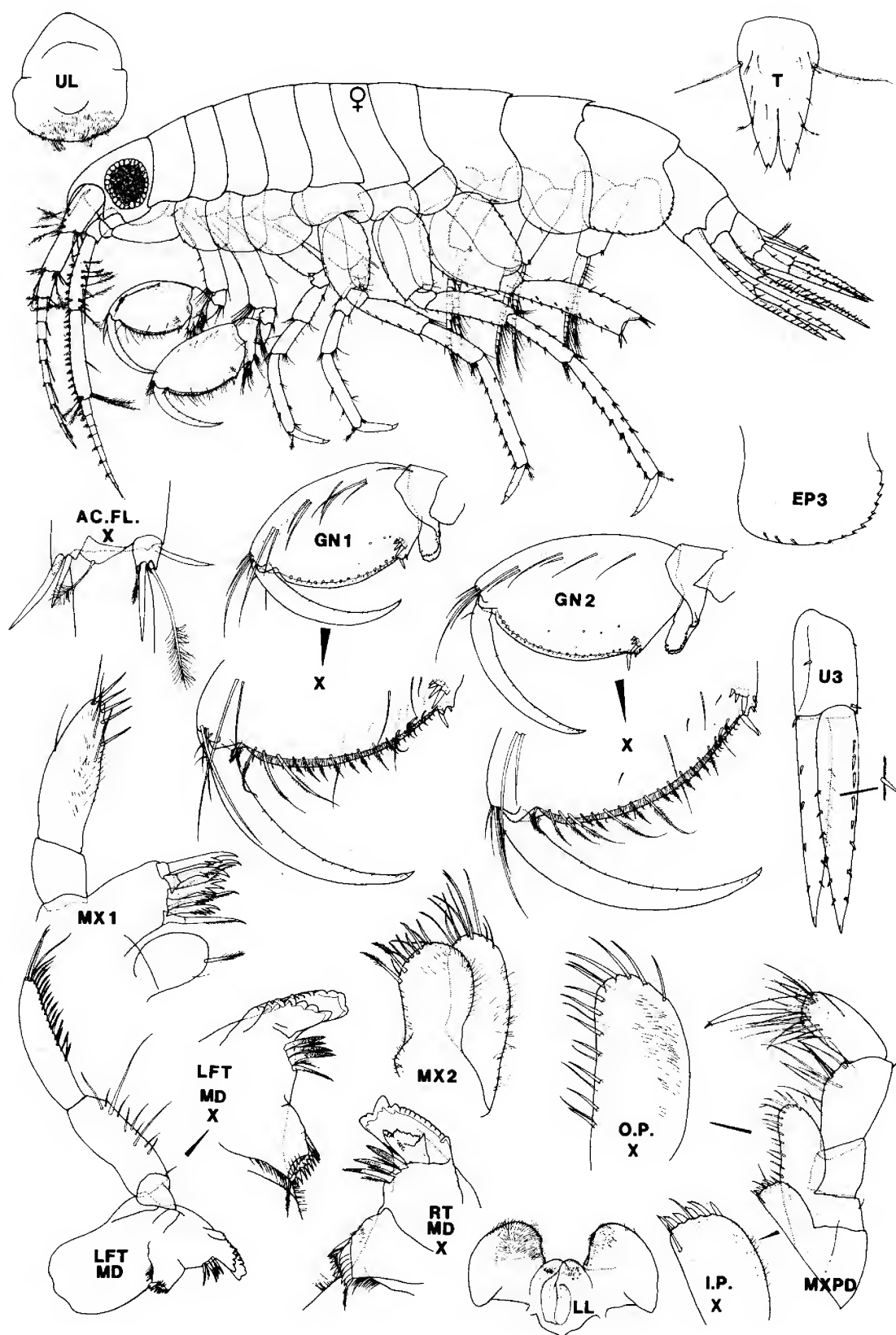


FIG. 23. *Rhachotropis conlanae*, n. sp. Female (4.5 mm). Boca de Quadra, Alaska, 29 m.

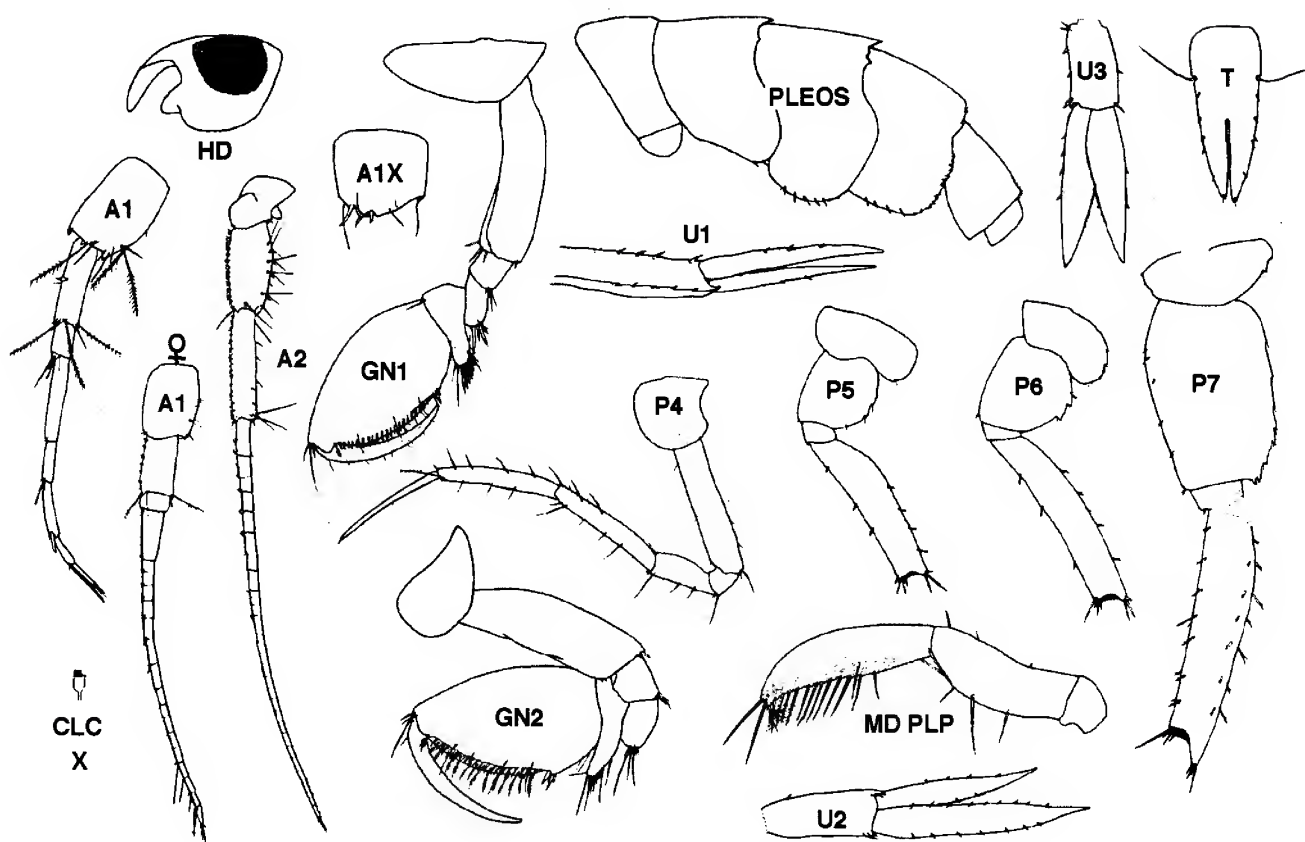


FIG. 24. *Rhachotropis luculenta* J. L. Barnard, 1969c. Male (4.6 mm)
Gulf of California. (modified from Barnard, 1969c)

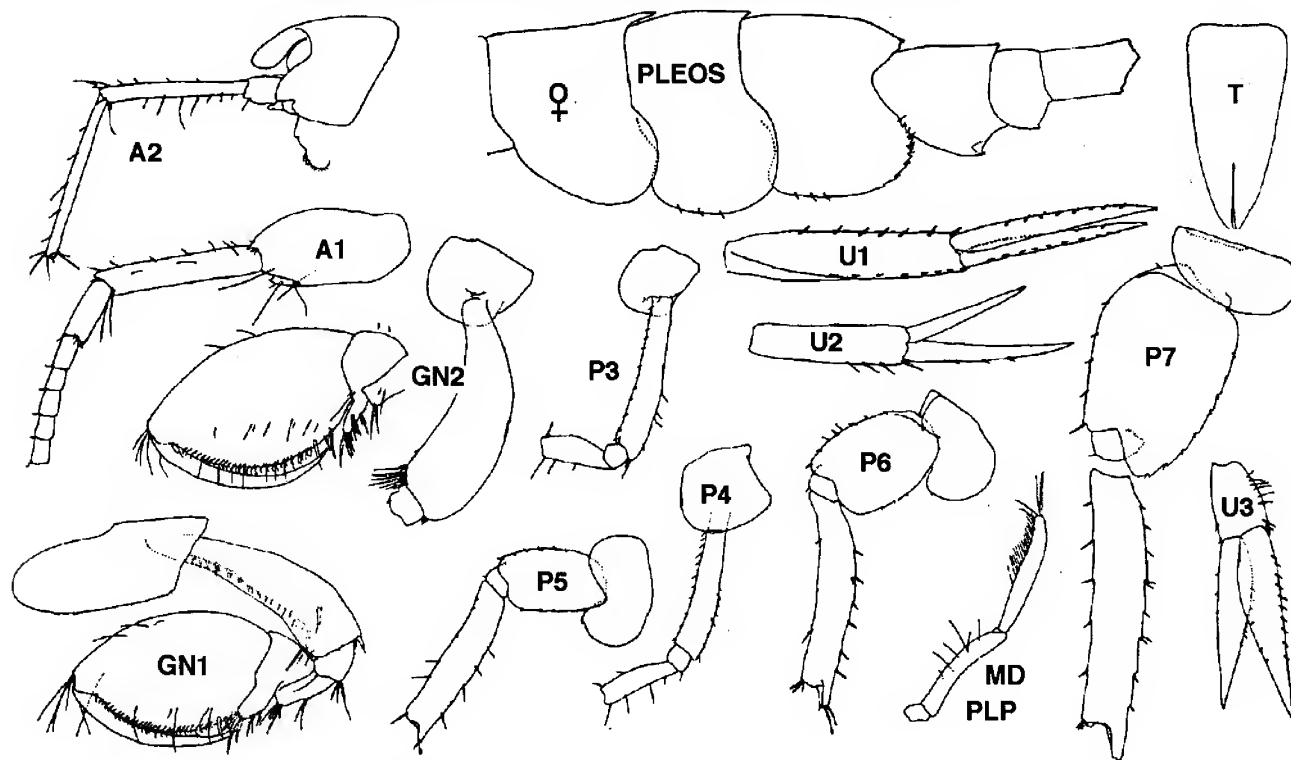


FIG 25. *Rhachotropis ludificor* J. L. Barnard, 1967. Male? (4.5 mm).
Off southern California, 1700+ m. (modified from Barnard, 1967)

Rhachotropis americana new species
(Fig. 26)

Material Examined:

BRITISH COLUMBIA: CMN Collections: NW of Englefield Bay, Queen Charlotte Ids., RBCM/CMN Stn 91-1-119, Deep water II, otter trawl, 0-1227 m, Mar. 21, 1991 - 1 female ov (11.3 mm), Holotype (slide mount); male (9.5 mm), Allotype (slide mount), 5 females, 1 MALE Paratypes; Off Frederick I., Q. C. I., Stn. 91-1-14 (53°57.00'N, 133°52.86'W to 53°57.63'N, 133°54.30'W) 0-1150 m otter trawl, Mar. 22/91 - 1 female.

Diagnosis. Female (11.3 mm) Holotype: Peraeon and urosome 1 smooth above. Pleon segments 1-3 with medium strong dorsal and dorso-lateral teeth, 2 largest. Rostrum short; anterior head lobe prominent, acute. Pigmented eyes lacking. Antenna 1 shorter than antenna 2, lacking calceolae; peduncular segments 1 and 2 medium, subequal, 3 elongate (>1/2 segment 2); flagellum 12-segmented; accessory flagellum very short, apex with plumose seta. Antenna 2 lacking calceoli; peduncular segments 4 and 5 slender, subequal, segment 4 with proximal posterior cluster of plumose setae; flagellum 16-segmented.

Mandible, molar small, subconical, grinding surface evanescent, replaced by several slender blades; spine row with 5-6 slender blades; left lacinia unevenly 5-dentate; right lacinia bifid; main cutting edge of incisor nearly smooth; palp slender, apically narrowing, segments 2 and 3 subequal in length. Maxilla 1, inner plate with 2 apical setae; palp slender, apex acute. Maxilla 2, inner plate broad, rounded, inner margin proximally with 2 longer plumose setae. Maxilliped palp strong, segment 2 little broadened; outer plate large, inner plate with 4-5 slender apical spines.

Coxa 1 strongly produced anteriorly, reaching tip of anterior head lobe, apex subacute, lower hind corner with single cusp. Coxae 2-4 shallow, broader than deep; coxa 4 excavate behind. Gnathopod 2 larger than gnathopod 1; basis heavier, lined with short spines; carpal lobes slender apices sparsely setose; propods slender ovate, hind margins short; palmar margins nearly horizontal, dactyl tip depression broad, with 2-3 inner marginal and 1 stouter outer marginal spine.

Peraeopods 3 and 4 slender, segment 4 distinctly shorter than segment 5; dactyls elongate (> segment 6). Coxae 5 and 6, hind lobes acute below. Peraeopods 5 and 6 slender, subsimilar in form and presumably length; bases slender, not lobate behind; dactyls slender. Peraeopod 7 very much larger and presumably longer (distal segments missing); basis medium broad, not lobed below.

Pleon plates 1-3 broad rounded and weakly spinose below; hind margin of plate 3 convex, with numerous medium serrations. Uropods 1 and 2, rami slender, not reaching tip of uropod 3; outer ramus of uropod 2 distinctly shorter than inner ramus. Uropod 3, outer ramus slightly the shorter; peduncle with acute inner marginal distal process. Telson elongate, nearly attaining tip of uropod 3, narrowly cleft

1/3 of length.

Coxal gills large, plate-like, not pleated. Brood plates on peraeopods 2-4 broad, on 5 broadly strap-like.

Male (9.5 mm): Antenna 1 not calceolate, peduncular segments 1 and 2 with strong posterior marginal clusters of brush setae; flagellum basally weakly callynophorate. Antenna 2 not calceolate; peduncular segments 3 and 4 with strong anterior marginal clusters of brush setae. Mandible, left lacinia 6-dentate; palp segment 3 slightly longer than 2, apex rounded.

Etymology. The species name alludes to its occurrence in coastal waters of Pacific North America.

Taxonomic and distributional commentary. *Rhachotropis americana* is known only from two localities off the Queen Charlotte Islands, B. C. It closely resembles *R. grimaldi* (Chevreux), previously recorded from the Sea of Okhotsk (Gurjanova, 1951), in characters of the key (p. 23), and in the strong postero-distal notch of coxa 1, but differs in the less rugose dorsum of head and anterior peraeonal segments, and the button-like (rather than linear) form of the accessory flagellum, among other differences. It is also similar to *R. multesimus* Barnard from Los Cedros Trench off central Baja California (below), but differs in characters outlined in the key.

Rhachotropis grimaldi Gurjanova
(Fig. 27)

?*Rhachotropis grimaldi* Gurjanova, 1955: 180, fig. 11.

non *Tritopsis grimaldi* Chevreux, 1887: 571.

non *Rhachotropis grimaldi* Ledoyer, 1982a: 239, fig. 162.—
Barnard & Karaman, 1991: 338.

Taxonomic and distributional commentary. Gurjanova (loc. cit.) has figured a medium large (15 mm) deep-water species from the Okhotsk Sea that lacks the pigmented eyes of the Mediterranean type regional species illustrated by Ledoyer (1982a). Although the two populations are obviously closely related, they appear to differ significantly in the form of the telson, dorsal armature of the pleon, and in a number of other features that would suggest that two distinct species are involved.

Rhachotropis multesimus Barnard
(Fig. 28)

Rhachotropis multesimus J. L. Barnard, 1967: 119, fig. 7.

Taxonomic commentary. This very small (3.8 mm) blind species from bathyal depths off Baja California, resembles *R. grimaldi* as illustrated by Gurjanova 1955 (above) except for the much less strongly developed teeth and spines of the body and appendages. The enigmatic *R. cervus* Barnard, 1957, from the same location, may be phylogenetically closest to *R. grimaldi* (Gurjanova) and to *R. multesimus*.

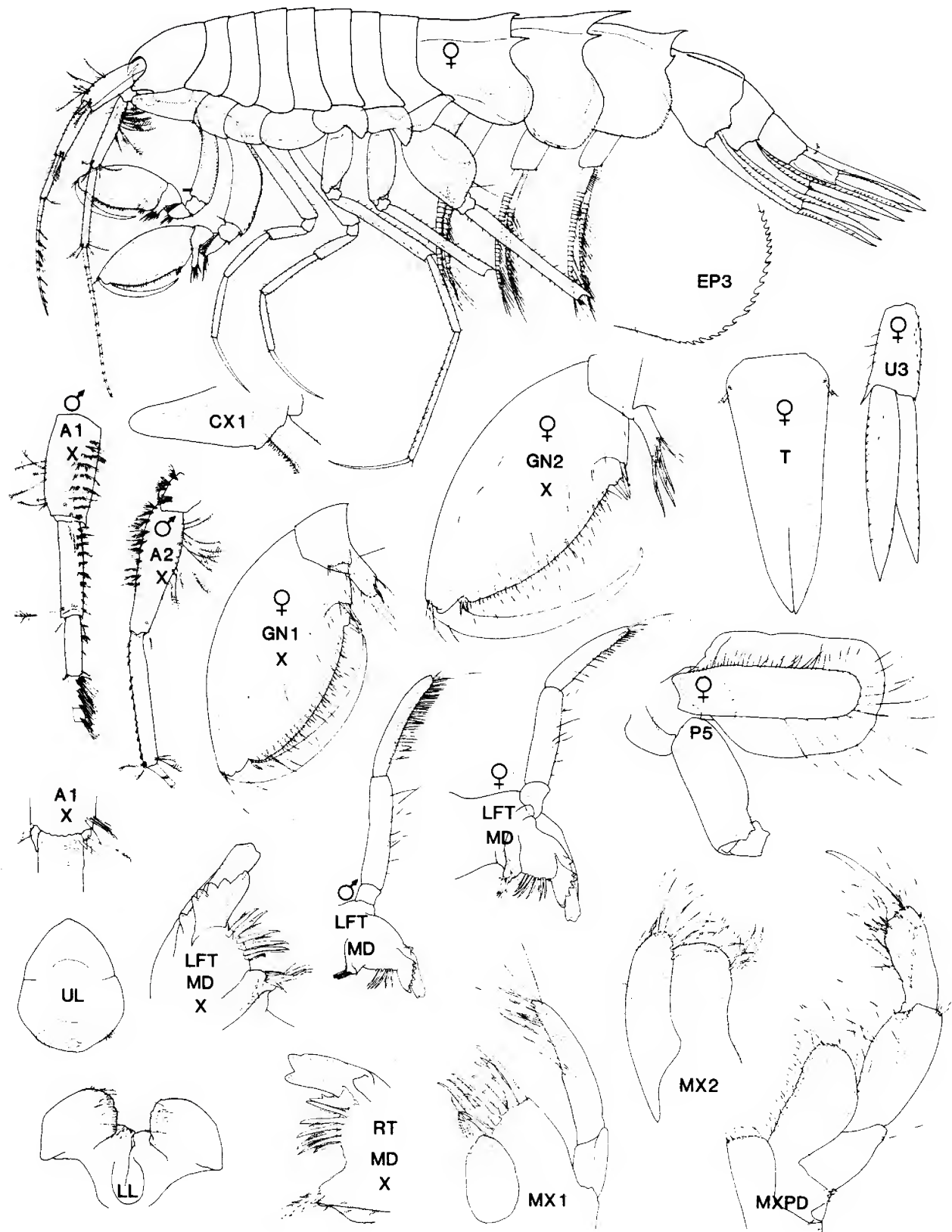


FIG. 26. *Rhachotropis americana*, n. sp. Female (11.3 mm); male (9.5 mm). NW of Englefield Bay B.C.

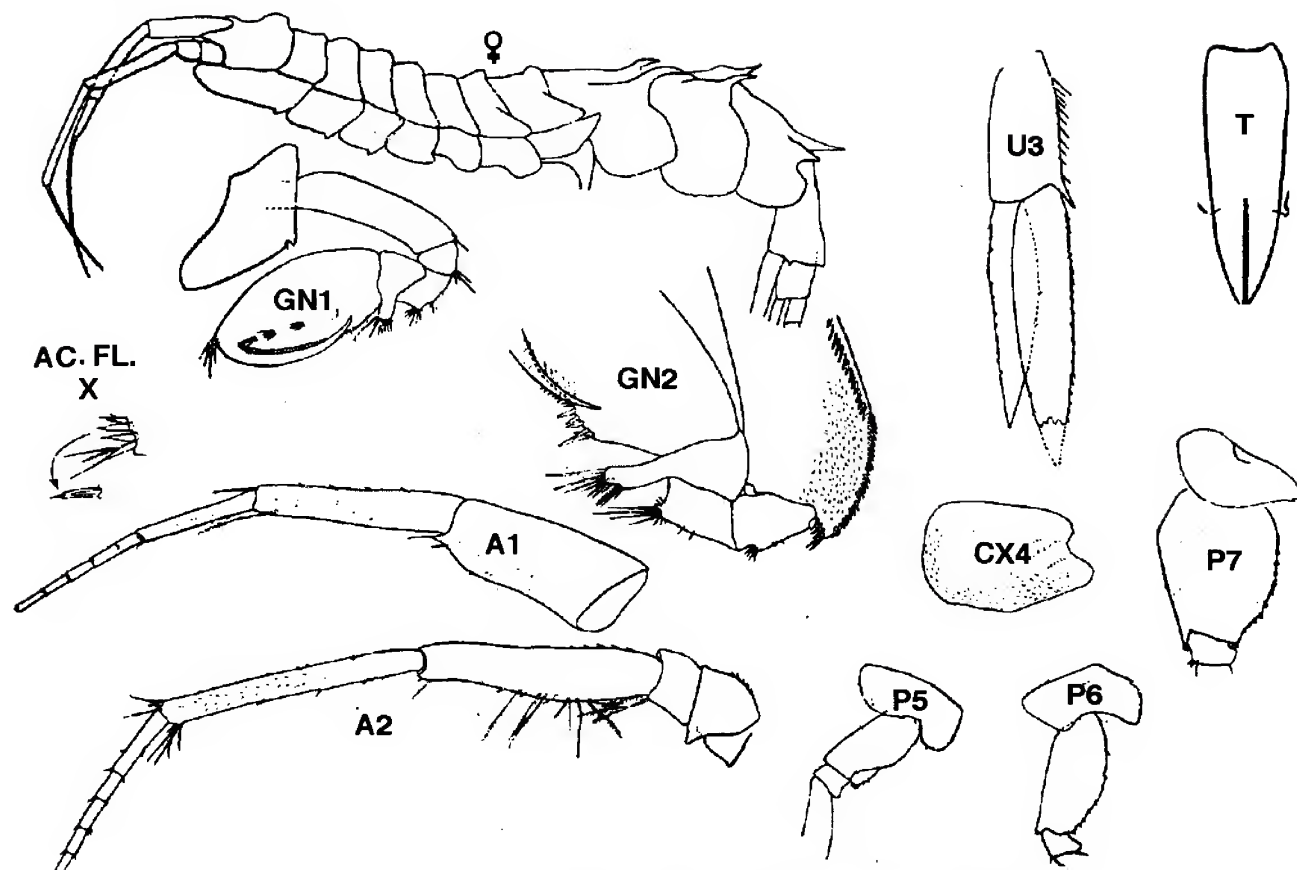


Fig. 27. *Rhachotropis grimaldi* (Chevr) Gurj. 1955. Female (15.0 mm)
Okhotsk Sea and N. Pacific (to 3000 m) (modified from Gurjanova, 1955)

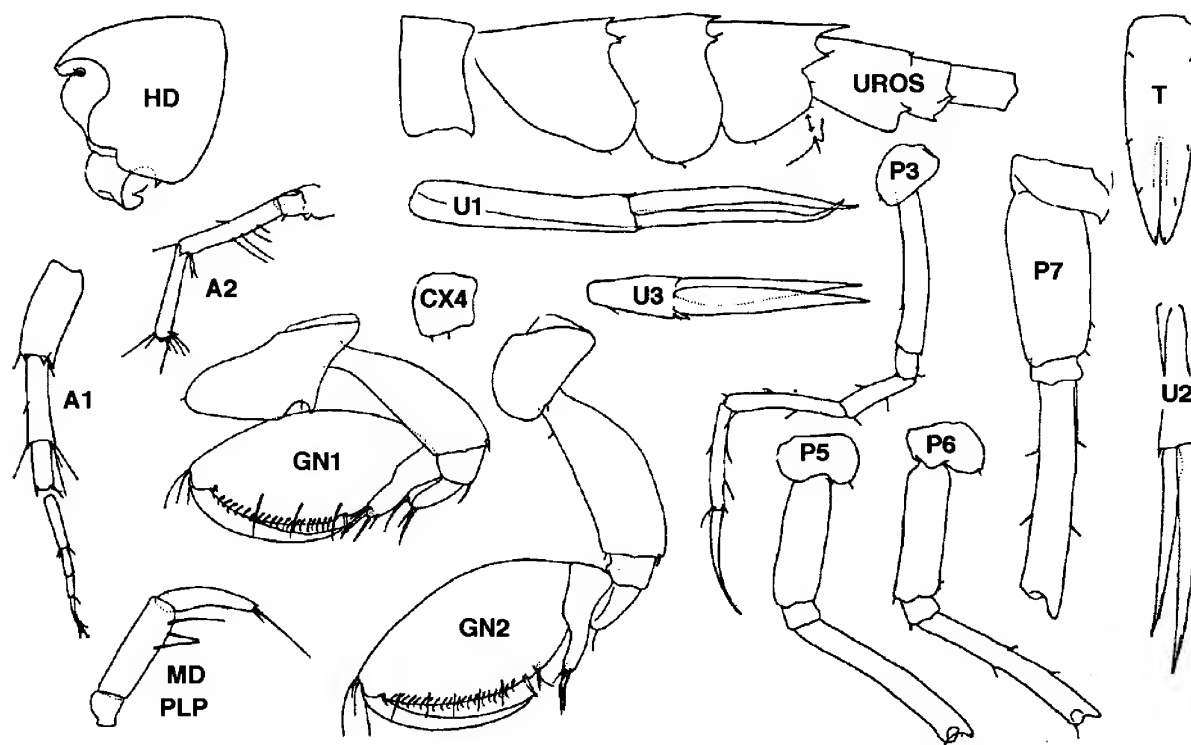


FIG. 28. *Rhachotropis multesimus* Barnard, 1967. Female? (3.8 mm)
off S. California, 1700+ m) (modified from Barnard, 1967)

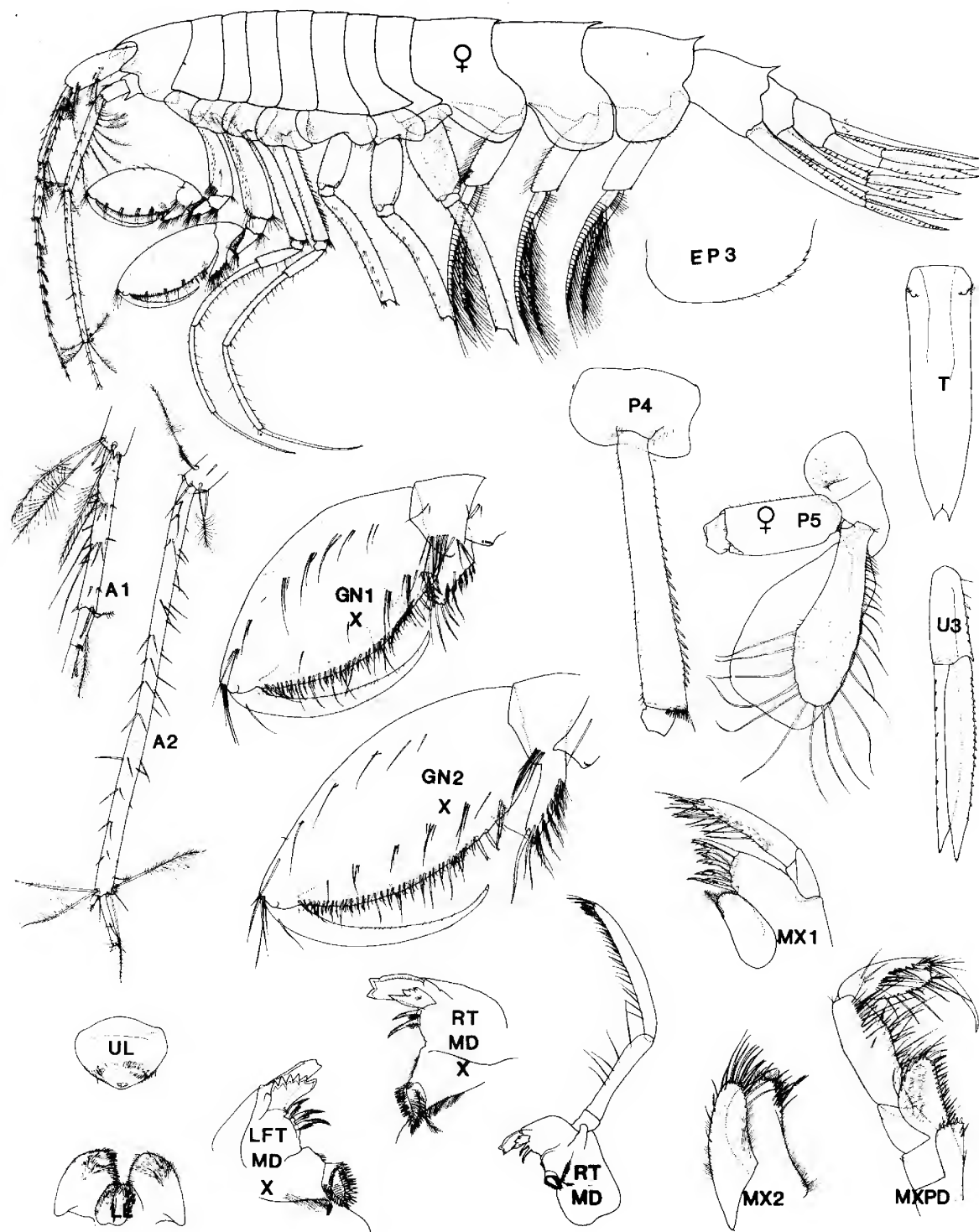


FIG. 29. *Rhachotropis distincta* (Holmes, 1908). Female ov. (9.0 mm). NW Englefield Bay, Q.C. I., B. C.

Rhachotropis distincta (Holmes)
(Figs. 29, 30)

Gracilipes distincta Holmes, 1908: 529, fig. 35.—Thorsteinson, 1941: 85 (key only).

Rhachotropis distincta Shoemaker, 1930: 316, figs. 41-44.—Birstein & Vinogradov, 1955: 276.—Birstein & Vinogradov, 1958: 248.—Barnard & Karaman, 1991: 338.

Material Examined:

BRITISH COLUMBIA: Queen Charlotte Islands, northwest of Englefield Bay ($53^{\circ}05.08'N$, $133^{\circ}00.08'W$ to $53^{\circ}06.58'N$, $133^{\circ}01.22'W$), RBCM/CMN Deepwater II Stn. 91-1-11, 0-1227 otter trawl, March 21, 1991. - 1 female (9.0 mm) (slide mount).

Diagnosis. Female (9.0 mm): Peraeon smooth above. Pleon segments 1-3 and urosome 1 each with posterior dorsal

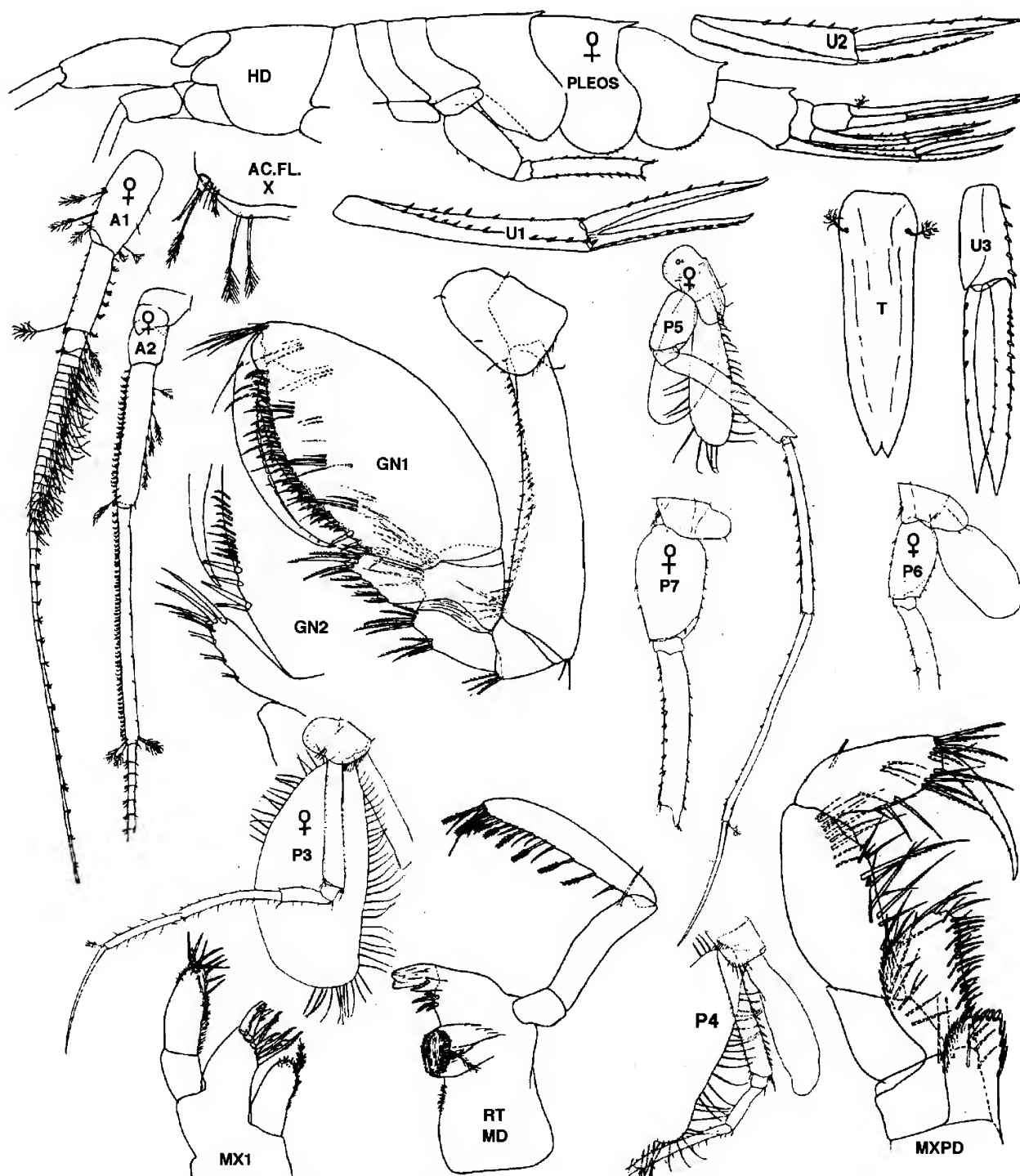


FIG. 30. *Rhachotropis distincta* (Holmes, 1908) Female ov (9.0 mm) Male (8.0 mm)
Cabot Strait. 378m (modified from Shoemaker, 1930)

mucronation. Rostrum medium strong, extending beyond acute anterior head lobe. Pigmented eyes lacking. Antenna slender, not calceolate in female. Antenna 1, peduncular segments 1 and 2 subequal in length, segment 3 elongate ($>1/2$ segment 2); flagellum 10-12 segmented; accessory flagellum minute, apex with spine and plumose seta. Antenna 2 longer than 1; peduncle 4 shorter than 5, hind margin lined with plumose setae; flagellum 12-14 segmented.

Lower lip tall, inner lobes distinct. Mandible, molar

narrowing to small grinding surface, margins lined with blades; spine row with 2-3 blades; left lacinia 6-dentate, right lacinia bifid; incisor cutting edge thickened; palp slender, segment 3 longer than 2. Maxilla 1, inner plate with long and short apical setae; palp slender. Maxilla 2, inner plate broader than outer, inner margin with longer plumose seta. Maxilliped palp strong, segment 3=2 and 3, slightly broadened; outer plate ordinary, inner plate with 5 apical short spines.

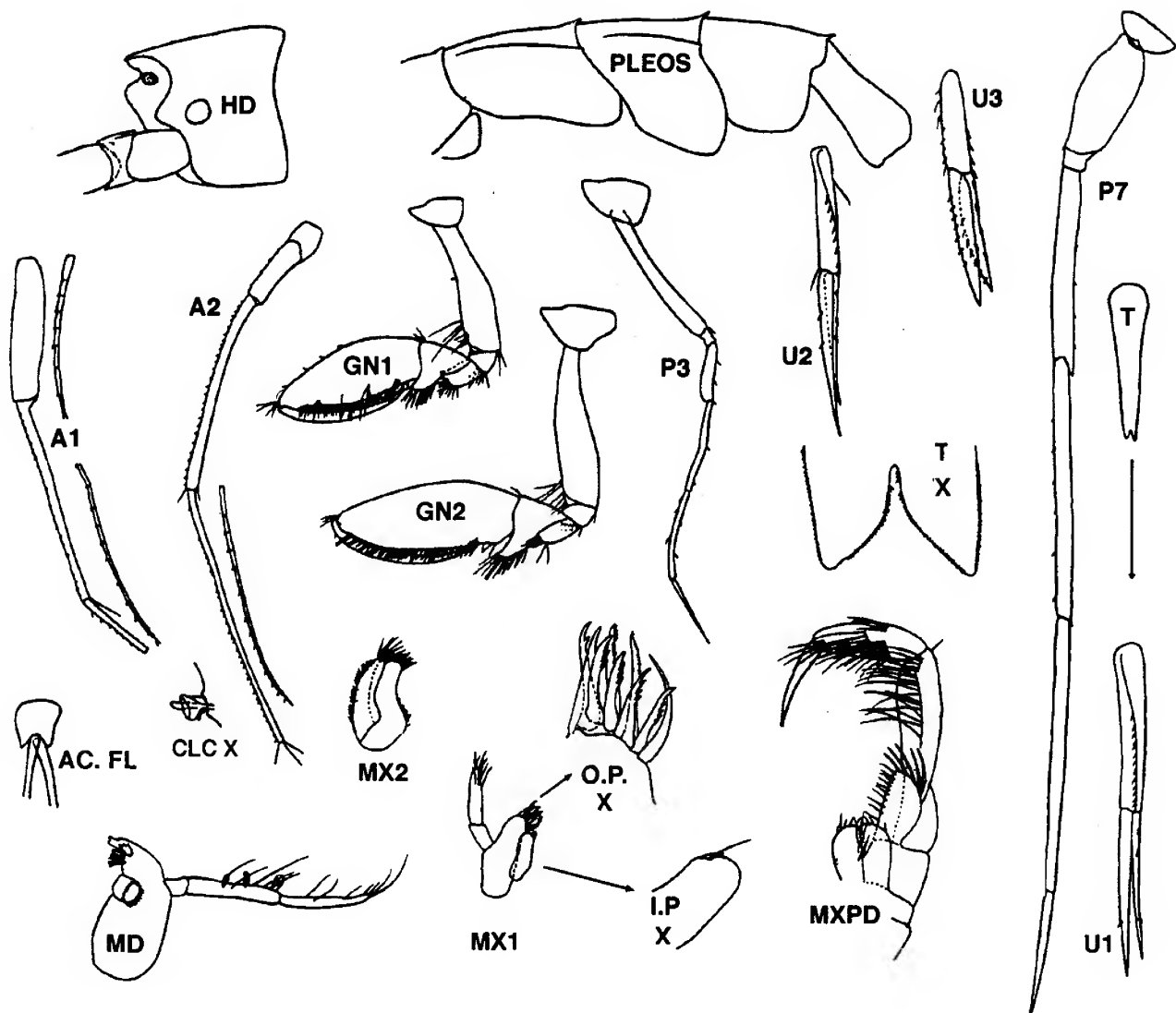


FIG. 31 *Rhachotropis natator* (Holmes, 1908). Female (13.0 mm) off S. California (1000+ m.) (modified from Barnard, 1954)

Coxae 1-4 shallow, broader than deep, not produced anteriorly; coxa 4 weakly excavate behind. Coxa 5 shallowly aequilobate. Gnathopod 2 larger than gnathopod 1; bases with antero-distal setal group and short-spinose anterior face; carpal lobes well developed, directed forwards under short posterior margin of propod; propods ovate, palmar margins oblique, dactyl tip depression with inner posterior group of 3-4 spines and 2-3 larger outer marginal spines.

Peraeopods 3 and 4 slender, elongate; segment 4 much shorter than segment 5; dactyls slender, longer than segment 6; basis of peraeopod 4 lined posteriorly with medium spines. Peraeopods 5-7 extremely elongate, increasing in size posteriorly; bases medium, not lobed below; dactyls very long, slender.

Pleon plates 1-3 broad rounded and weakly spined below; posterior margin of plate 3 weakly serrate. Uropods 1 and 2, peduncles longer than narrowly lanceolate rami, tips reaching to end of uropod 3; outer ramus shorter than inner. Uropod 3, rami somewhat broadly lanceolate, subequal,

margins weakly spinose. Telson elongate, parallel-sided, narrowing relatively abruptly, apex notched.

Coxal gills sac-like, broadest on peraeopods 5 and 6. Brood plates very large and broad on peraeopods 2-4, medium broad on peraeopod 5, margins strongly setose.

Male (8.0 mm): Antenna 1, peduncular segment 2, hind margins with a few brush setal clusters; flagellum elongate, basal 20 segments forming a weak callynophore, distal segments calceolate. Antenna 2, anterior margins of peduncular segments 4 and 5 lined with brush setae; flagellum elongate, segments calceolate.

Taxonomic and distributional commentary. *Rhachotropis distincta* occurs broadly across the boreal North Pacific and North Atlantic oceans but is apparently less frequently encountered in the Pacific than is *R. natator*. The present material compares closely with that figured by Holmes (loc. cit.) from southern California, and the detailed figures of material from the western North Atlantic region provided by Shoemaker (loc. cit.).

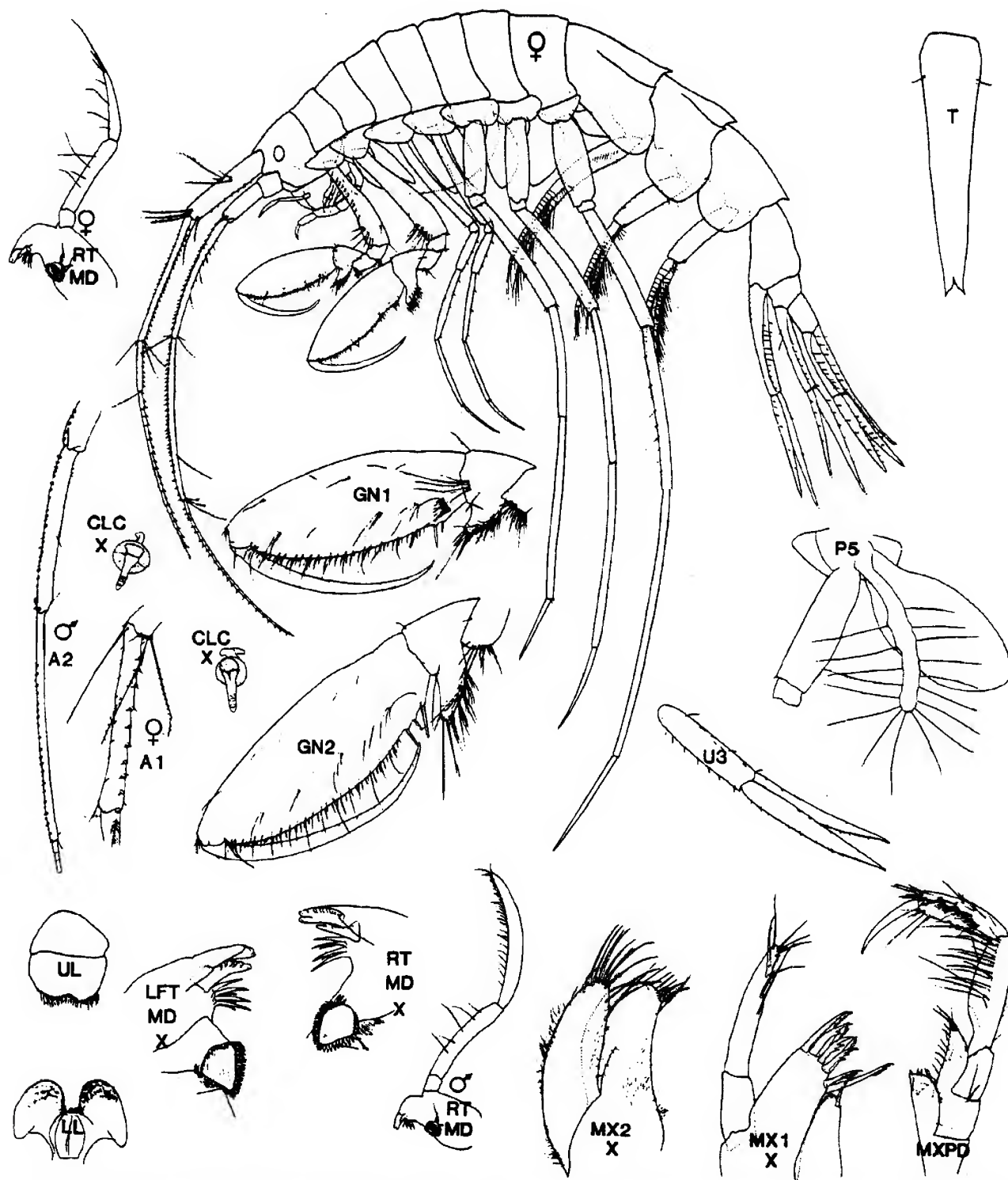


FIG. 32. *Rhachotropis natator* (Holmes, 1908). Female ov. (13.0 mm). Off Vancouver I., B. C. 1800 m

Rhachotropis natator (Holmes)
(Figs. 31, 32)

Gracilipes natator Holmes, 1908: 527, fig. 32-34.—Thorsteinson, 1941: 85, figs. 67-70.

Rhachotropis natator Barnard, 1954: 54, pl. 6.—Birstein & Vinogradov, 1955: 275.—Birstein & Vinogradov, 1958: 247.—Birstein & Vinogradov, 1960: 225. Barnard & Karaman, 1991: 338.

Material Examined:

BRITISH COLUMBIA: Queen Charlotte Islands: Off Tasu Sd (52°38.72'N, 132°05.79'W to 52°38.31'N, 132°07.90'W) IKMT 0-520 m., RBCM/CMN Stn. 91-1-09 - 1 male, 1 female; Off Kunghit I., (52°00.39'N, 131°23.97'W to 52°00.55'N, 131°30.90'W) IKMT 0-510 m., RBCM/CMN Stn. 91-1-03, Mar. 19, 1991 - 6 females; off Hippa I. (53°30.39'N, 133°26.35'W to 53°34.5'N, 133°30.20'W) IKMT 0-660 m., RBCM/CMN Stn 91-1-12, Mar. 21, 1991-4 males,

,6 females (1 male, 1 female slide mts).

Off Vancouver I., above Endeavour Ridge (47° 58'N., 129° 06' W), IOS Stns, June 18-19, 1990: LC 90-3 Tow 006 Net 2, 1870-1900 m - 1 male (12.0 mm) (slide mount). Ibid, July 17-19, 1991. IOS Stn. 91-12: tow 1, net 5, 1706-704 m. - 2 males; tow 2, Net 1, 0-1900 m. - 1 female ov (13.0 mm) (slide mount), 1 female br. I (11.5 mm); tow 3, net 3, 1985-1787, 2 females, 1 male; Tow 4, net 3, 2306-1925m - 1 female; tow 4, net 6, 713-560m - 1 male. Collections of the Institute of Oceanography, Sidney, B. C.

Diagnosis. Female (13.0 mm): Peraeon segments 1-7 and urosome segment 1 generally smooth dorsally. Pleon segments 1 & 2 with low mid-dorsal and dorso-lateral mucronations; pleon 3 with small dorsal tooth. Rostrum very short, extending little beyond short anterior head lobe. Pigmented eyes lacking. Antennae very slender and elongate, calceolate on peduncles only; calceoli with broad orbicular receptacle and distal elements in a rod-like central column. Antenna 1, peduncular segment 2 elongate, 1.5X segment 1; segment 3 long, ~ 1/3 segment 2; flagellum 15-segmented; accessory flagellum minute, with apical spine and setae. Antenna 2 longer than 1, peduncle 3 elongate, segment 5 > 4; flagellum 25-segmented, basally calceolate.

Upper lip slightly incised below. Lower lip, inner lobes narrow, distinct. Mandible, molar stout, grinding surface large, diamond shaped, margins lined with short blades; spine row with 4 slender blades; left lacinia 6-dentate; right lacinia bifid; incisor denticulate; palp slender, segment 3 shorter than 2. Maxilla 1, inner plate tall, with 1 apical seta; outer plate with 9 apical slender spines; palp slender. Maxilla 2, plates slender, setae apical. Maxilliped, palp large, segments 2 & 3 not broadened; outer plate slender; inner plate with 1-2 short apical spines.

Coxae 1-4 very small, shallow, anterior margin somewhat produced; coxae 5 and 6 shallowly aequilobate. Gnathopod 2 larger than 1; bases stout, with antero-distal setae; carpus produced below and under short hind margin of palp; propods elongate-ovate, palmar margins elongate, nearly horizontal, dactyl-tip depressions broad, with 1-2 outer marginal spines.

Peraeopods 3 and 4 very slender, segment 4 much shorter than 5; dactyls shorter than segment 6. Peraeopod 5-7 very slender and elongate, increasing in length posteriorly; bases narrow, not lobate behind.

Pleon plates 1-3 broad, differing in form, 2 deepest; 3 rounded; hind margin not serrated. Uropods 1 and 2, rami narrowly lanceolate, margins weakly spinose, outer ramus shorter than inner. Uropod 3, rami subequal, margins very weakly spinose. Telson very elongate, narrowing distally, reaching nearly to tip of uropod 3, apex broadly notched.

Coxal gills sac-like, broadest on peraeopod 6, smallest on peraeopod 7. Brood plates broad, narrow on peraeopod 5.

Male (12.0 mm): Similar to female but differing in the flagellum of antenna 1 that is proximally weakly

callynophorate, and distally weakly calceolate. Mandibular palp, segment 3 elongate, not reduced.

Taxonomic and distributional commentary. *Rhachotropis natator* is apparently widespread in offshore waters of the boreal North Pacific Ocean, in depths of 1000-5000 m. The present material compares closely with the 14 mm male figured by Thorsteinson (loc. cit.) from off the coast of Washington State, and the 13.0 mm female illustrated by Barnard (loc. cit.) from waters off southern California. Material from the western Pacific region, for which numerous offshore collection stations are provided by Birstein and Vinogradov (loc. cit.) has not been sufficiently well figured to facilitate detailed comparison with eastern Pacific material.

DISCUSSION AND CONCLUSIONS

This systematic study has examined material of 14 species (in 5 genera) of amphipod crustacean of the family Eusiridae that occur in shelf and offshore waters of the North American Pacific region, from the Bering Sea to central California. The taxonomy and distributional ecology of this limited assemblage can now be analyzed in relation to an overall amphi-North Pacific eusirid fauna of some 35 species (in 10 genera), a number that represents about 30% of the species of family Eusiridae world-wide. As noted in station lists of the previous descriptive accounts, species of Eusiridae tend to occur in relatively deep benthic and offshore bathyal and bathypelagic environments, and are thus not well represented in present regional amphipod collections that were obtained mainly from shallow water and littoral marine habitats.

However, despite the limited nature of the material at hand, the possible broader phyletic and biogeographic significance of these morphological and distributional findings may be analyzed on a numerical basis. A modification of the phenetic UPGMA (cluster analysis) system of Sneath and Sokal (1973) has been employed reasonably effectively in earlier studies of this type (e.g. Bousfield and Jarrett, 1994; Bousfield & Hendrycks, 1994) and is utilized here. In this system, the character states are ordered on a presumed phyletic basis, and from this can be developed an overall criterion of phyletic similarity termed the Plesio-Apomorphic (P.-A) Index in which low numbers signify phyletically primitive, and high numbers relatively advanced, species or taxonomic groups.

Within the family Eusiridae, analysis of morphological similarities is based on 20 characters, and corresponding 40 paired character states, of the 13 component genera world-wide (Table I, p. 48). The characters selected include a mixture of conspicuous body features, well described and illustrated in the literature, as well as more cryptic, but possibly more phyletically significant features such as those of the mouthparts. The latter have been summarized especially helpfully by Barnard and Karaman (1991), although

TABLE I. GENERA OF EUSIRIDAE: CHARACTERS AND CHARACTER STATES

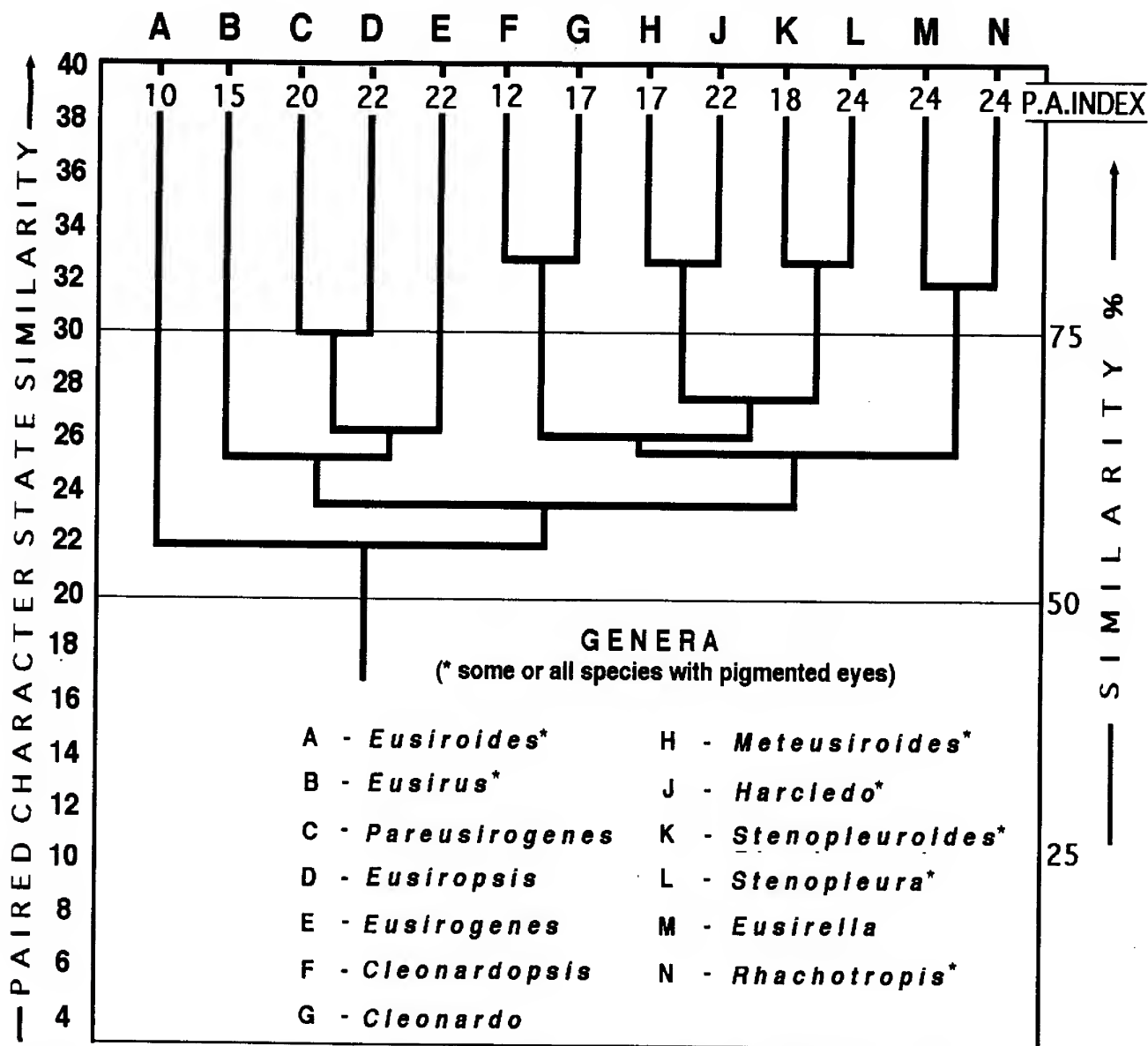
CHARACTER	CHARACTER STATE VALUE		
	Plesiomorphic 0	Intermediate 1	Apomorphic 2
1. Rostrum, length	long (~ length of head)		short (<anterior head lobe)
2. Pigmented eyes	present		absent
3. Antenna calceolate	calceolate	weakly calceolate	calceoli lacking
4. Accessory flagellum	present, 1-2-segmented	scale-like	lacking
5. Peraeon 5-7 dorsally toothed	strongly	weakly	smooth
6. Pleon dorsally toothed	strongly	weakly	smooth
7. Lower lip, inner lobes	weak		strong
8. Mandibular molar, triturating surface	large		small
9. Mandibular palp, segment 3	ordinary (< segment 2)		slender (> segment 2)
10. Maxilla 1, number of inner plate setae	4+	2-3	0-1
11. Maxilla 1, number of outer plate spines	11		9
12. Maxilla 2, width of inner plate	~ outer plate		>> outer plate
13. Coxae 1-4, depth	deeper than wide	squarish	shallow, depth < width
14. Gnathopods 1 & 2 propod & carpus, form	ordinary, carpus thick		"eusiroidean", carpus slender
15. Gnathopods, armature of palmar margin	heavy spines	few spines	setae only
16. Peraeopods 3-4, length of dactyls	short, (< 1/3 segment 6)		elongate (~= segment 6)
17. Peraeopods 5-7 form and length	homopodous in form & length		heteropodous in form & length
18. Uropods 1 & 2, armature, apex of rami	lanceolate, no spines		spinose
19. Uropod 3 rami, inner margins	setose & spinose		spinose only or unarmed
20. Telson, length	elongate, length >3X width		short, length < 2X width

the basic pertinent references have been consulted wherever possible. In evaluating some character states, an intermediate character state did not exist, and was therefore not given in the table.

Within the resulting phenogram of genera (Fig. 33), three main groups may be recognized that cluster between the 50 and 60% similarity levels. These comprise the primitive relatively isolated genus *Eusiroides* on the left (P.

A. Index of 10), a relatively advanced *Cleonardo-Rhachotropis* group on the right (P. A. Indices mainly of 17-24, excluding the monotypic genus *Cleonardopsis*), and an intermediate *Eusirus* group on the left centre (P. A. Indices of 15-22). Species of the genus *Eusiroides* are characterized by pigmented eyes, distinct accessory flagellum, deep coxae, subsimilar spiny-palmed gnathopods, short stout short-dactylate peraeopods, and setose rami of uropod 3, among

FIG. 33. PHENOGRAM OF GENERA: FAMILY EUSIRIDAE



other plesiomorphic character states. With few exceptions the 16 described species are littoral, along tropical and warm-temperate, high salinity coasts of the Atlantic, Indian, and Pacific oceans. These character states are similar to those of members of families Pontogeneiidae and Calliopiidae within superfamily Eusiroidea.

The *Eusirus* group is characterized mainly by the "eusirid" form of the gnathopod propods, in which the deep, smooth-palmed propod is subtended from the tip of the long slender narrow-lobed carpus. Of the 32 described world species, two-thirds are species of *Eusirus*, whose members are relatively large bodied, eyed, and sublittoral and epibenthic. The remaining eight species, within *Pareusirogenes*, *Eusiropsis*, and *Eusirogenes*, are relatively small, eyeless, more slender bodied and uncarinated, that are meso- or bathypelagic in life style. The *Cleonardo-Rhachotropis* group encompasses 8 genera and about 70

world species whose members are mostly meso- and bathypelagic. The gnathopods are subsimilar but non-eusirid in form, the carpus simple and lobate behind, and the propodus usually with an elongate, marginally spinose, and very oblique palm. The group encompasses 4 sets of genera: (1) a primitive *Cleonardo* subgroup of about 10 eyeless, homopodous, bathypelagic world species, (2) a more advanced *Harcledo-Stenopleura* complex of 4 monotypic generic whose members are mesopelagic, and have small bodies, with shallow coxae, pigmented eyes, and short telsons, but the antennae lack calceoli and accessory flagellum., and (3) an advanced but amorphous *Eusirella* complex of about 55 world species of which 9/10 are species of *Rhachotropis* (analyzed below). "Classical" morphological analysis of *Eusirella* and *Rhachotropis* would suggest rather different basic morphologies between the two genera, although similarities in mouthpart structure such as the

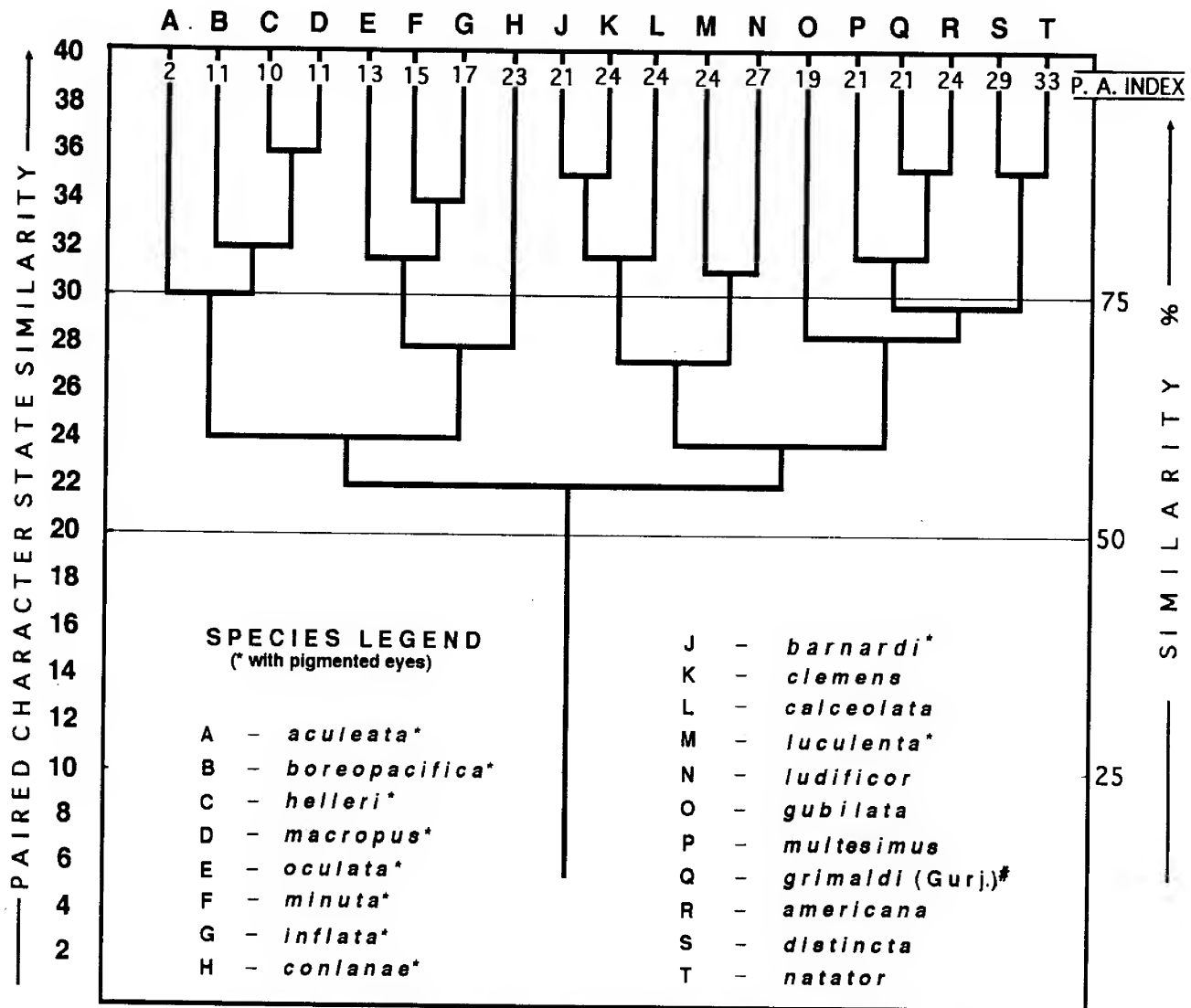
TABLE II. SPECIES OF *RHACHOTROPIS* : CHARACTERS AND CHARACTER STATES

CHARACTER	CHARACTER STATE VALUE		
	Plesiomorphic 0	Intermediate 1	Apomorphic 2
1. Rostrum, length	long (~ length of head)		short (<anterior head lobe)
2. Pigmented eyes	present		absent
3. Peraeon 5-7 dorsally toothed	strongly	weakly	lacking
4. Pleon 1-2, mid-dorsal mucronation	strong	weak	lacking
5. Pleon 1-2, dorso-lateral mucronation	strong	weak	lacking
6. Pleon 3, mid-dorsal mucronation	strong	weak	lacking
7. Pleon 3, dorso-lateral mucronation	strong	weak	lacking
8. Urosome 1, mid-dorsal tooth	strong	weak	lacking
9. Antenna 1, length of peduncular segment 3	very short (<1/4 segment 2)		long (~1/3 segment 2)
10. Gnathopods 1 & 2, propods	subequal		unequal in size and form
11. Peraeopods 3 & 4 segment 4: segment 5	subequal		segment 4 << 5
12. Peraeopods 3-4, length of dactyls	short, (< 1/3 segment 6)		elongate (~= segment 6)
13. Coxae 1-4, depth	deeper than wide	squarish	shallow, depth<width
14. Peraeopod 7, width of basis	broad, lobate below		narrow, not lobate below
15. Pleon plate 3 hind corner	squarish		strongly rounded
16. Uropod 1, length peduncle	>>inner ramus		~=inner ramus
17. Uropod 2, length inner ramus	long, attains tip of uropod 3		short, << tip of uropod 3
18. Uropod 3 rami, inner margins	setose & spinose		spinose only or unarmed
19. Telson, length	elongate, length >3X width		short, length ~2X width

relatively well developed inner lobes of the labium, and the 9-dentate outer plate of maxilla 1, would seem basic. However, basic differences (in peraeopods 3 and 4) may well have been masked in this analysis by instances of convergence and superficial similarity in body form and structure of the posterior peraeopods, uropods, and telson, etc, in various bathypelagic members of *Rhachotropis* resulting from convergent similarities in life style. More extensive conclusions would depend on more detailed morphological examination,

involving all members of both generic groups, well beyond the scope of this limited regional study.

The morphological relationships of North Pacific species within the relatively advanced genus *Rhachotropis* may be analyzed numerically on the basis of 20 characters and corresponding character states outlined in Table II (above). The characters selected are mainly superficial and conspicuous features of the body and appendages rather than mouthparts and reproductive features that may actually

FIG. 34. PHENOGRAM OF NORTH PACIFIC SPECIES OF *RHACHOTROPIS*

Includes *R. cervus* J. L. Barnard 1967 from Cedros Trench, Baja California?

prove more significant phylogenetically. However, the "high profile" characters tend to be described and illustrated more consistently and more completely in the available reference works and thus provide a more reliable basis for comparison between all species analyzed numerically here.

The resulting semi-phyletic phenogram is shown in Fig. 34 (above). As noted below, the 20 regional species (including the problematical *R. cervus*) represent about 40% of the known world species. This "breakout" also includes equal numbers having, or lacking, pigmented eyes, a feature that corresponds essentially with "shelf" or coastal species, and "bathyal" or deep-water species, respectively. Clustering between the 55 and 75% similarity levels are two main groups, a relatively primitive "*aculeata*" assemblage of 8 species on the left (P. A. indices of 2-23) and a relatively advanced "*natator*" assemblage of 11 species on the right (P. A. Indices of 19-33). The *aculeata* group tends to be of larger body size and more strongly toothed dorsally, and have pigmented eyes and more strongly calceolate antennae.

Species of the *natator* group are of smaller body size and weaker dorsal mucronation (peraeon generally smooth), the antennae are more frequently acalceolate and, with few exceptions, lack pigmented eyes.

The "*aculeata*" subgroup contains two distinct subclusters, a primitive *aculeata-macropus* group on the left (P. A. indices of 2-11) and a more advanced *oculata-inflata* group on the right (P. A. Indices of 13-23). The former species tend to be of larger size (10.5 - 40 mm in body length) are strongly toothed on pleon and urosome, and the telson is elongate. The latter species are typically small (3.8 - 12 mm in body length), the urosome lacks a dorsal tooth, and the telson is relatively short.

The "*natator*" group similarly contains two distinct subclusters, a slightly more primitive *clemens-ludificor* group on the left (P. A. indices of 21-27) and a more advanced *grimaldi-distincta* group on the right (P. A. Indices of 19-33). The former species tend to be of smaller size (3.8-8.7 mm in body length), are more weakly carinate on the pleon,

TABLE III. DISTRIBUTION OF NORTH AMERICAN PACIFIC EUSIRIDAE

SPECIES	NORTH PACIFIC SUBREGION								
	1	2	3	4	5	6	7	8	9
I. <i>Eusiroides</i>									
<i>japonica</i> Hirayama, 1985	X								
<i>monoculoides</i> (B'n'd, 1969)									X
II. <i>Eusirus</i>									
<i>hirayamae</i> , n. sp.	X								
<i>columbianus</i> , n. sp.				X	X	X			
<i>cuspidatus</i> Koyer, 1845		x?	X						
<i>bathybius</i> B. & V., 1960	X								
<i>fragilis</i> B. & V., 1960	X								
III. <i>Pareusirogenes</i>									
<i>carinatus</i> B. & V., 1955		X							
V. <i>Eusiroopsis</i>									
<i>riisei</i> Stebbing, 1897	X								
IV. <i>Eusirogenes</i>									
<i>homocarpus</i> B. & V., 1955	X								
VI. <i>Cleonardo</i>									
<i>longisetosa</i> Chevreux, 1908		X							
<i>macrocephala</i> B. & V., 1955		X							
<i>moirae</i> , n. sp.					x				
VII. <i>Harcledo</i>									
<i>curvidactyla</i> (Pirlot, 1934)		X							
VIII. <i>Stenopleura</i>									
<i>atlantica</i> Stebbing, 1888	X								
IX. <i>Eusirella</i>									
<i>multicalceola</i> (Thorst, 1941)	X	X			X	X			X
<i>longisetosa</i> B. & V., 1960	X								
X. <i>Rhachotropis</i>									
<i>aculeata</i> (Lepechin)		X	X						
<i>americana</i> , n. sp.					X				
<i>barnardi</i> , n. sp.					X?	X	X		
<i>boreopacifica</i> , n. sp.					x?	X			
<i>helleri</i> (Boeck)		X	X?						
<i>macropus</i> Sars		X	X?						
<i>oculata</i> (Hansen, 1888)		X?	X		x?	X	?	X	
<i>minuta</i> , n. sp.						X			
<i>inflata</i> (Sars, 1883)		X			x?	x?	X?		
<i>conlanae</i> , n. sp.				X					
<i>clemens</i> Barnard, 1967									X
<i>calceolata</i> , n. sp.									X
<i>luculenta</i> Barnard, 1969									X
<i>ludificor</i> Barnard, 1967									X
<i>gubilata</i> Barnard, 1964							x?		
<i>grimaldi</i> (Gurjanova, 1951)		X							?
<i>multesimus</i> Barnard, 1967									X
<i>distincta</i> (Holmes, 1908)		X			X	X			X
<i>natator</i> (Holmes, 1908)	X	X			X	X	x?		X

LEGEND: 1 - Southern Japan; 2 - Okhotsk, N. Japan; 3 - S. Chukchi & Bering Seas; 4 - S.E. Alaska; 5 - N. Brit. Columbia; 6 - S. Brit. Columbia; 7 - Wash.-Oregon; 8 -N. Calif.; 9. - S. and Baja Calif.

have relatively short rami of uropods 1 & 2, short peduncular segment 3 of antenna 1, some members are oculate, and all are taken almost exclusively in benthic samples. Members of the latter group (except for the small benthic *R. multesimus*), however, tend to be of medium size (11-17 mm), are more strongly toothed on the pleon, have longer uropod rami, and longer segment 3 of antenna 1, are exclusively eyeless, and are usually taken planktonically in the open water column.

This limited semi-phyletic analysis suggests a direct relationship between morphology and life style within *N.* Pacific members of the genus *Rhachotropis*. The coastal shelf, benthic and epibenthic species tend to be relatively large, oculate, processiferous, and spiny-limbed animals that become smaller, more weakly spinose, and anoculate in the most abyssal members. Bathypelagic members are of intermediate size and body armature but more slender-bodied and slender-limbed, exclusively anoculate, and generally most advanced phyletically. Such trends might indicate that the fully planktonic life style is a secondary development, and a possible basis for further formal subdivision within the genus *Rhachotropis*.

Biogeographic Analysis

The distribution of 36 species of family Eusiridae across the North Pacific region is represented in Table III (p. 52). The data were derived mainly from the literature, and the balance from the records of present material. A total of 22 species in 5 genera are now known from the North American Pacific region (sub regions 3-9) and about half the North Pacific total (18 species) have actually been recorded from the present study region (sub regions 3-7) from which specimens have actually been collected and examined.

The primitive benthic genus *Eusiroides* is represented on both Asiatic and N. American shores by single species that are restricted to the warmest and most southerly fringes (sub regions 1 and 9). Along more northerly and colder shores of both coasts, their ecological niches are presumably filled by hosts of "swash zone" pontogeneiid and calliopeiid eusiroidean counterparts.

The genus *Eusirus*, containing about 24 described world species, is moderately speciose in Arctic and eastern North Atlantic (including Mediterranean) sublittoral habitats. In the North Pacific, however, it is apparently restricted to single shelf species on each of the Asiatic and North American coasts, and two bathyal species along the Asiatic coast. The large arctic species, *E. cuspidatus*, penetrates only into the Bering Sea region.

With respect to the occurrence of offshore meso- and bathypelagic eusirids, a rich fauna of monotypic and near-monotypic eusirid genera has been discovered off the Asiatic coast, especially over the Kurile-Kamchatka Trench, and off the southeastern coast of Japan (genera III to XI, sub

regions 1 and 2). The studies of Birstein and Vinogradov (1955, 1958, 1960, 1964) have been instrumental in describing and analyzing this rich fauna both systematically and biogeographical. However, the paucity of counterpart records from the northeastern Pacific region (sub regions 4-8) poses limits to the present biogeographical analysis. The hiatus may reflect, at least in part, a deficiency in deep-sea biological sampling off the Pacific coast of the United States and Canada to date, or a delay in working up and publishing upon collections already at hand.

With respect to overall distribution, however, analysis of Table III reveals that the genus *Rhachotropis* dominates the North Pacific fauna of eusirid amphipods, both benthically and pelagically. In the northeastern Pacific region, the 15 species of *Rhachotropis*, from all habitats and life styles, represents more than two-thirds of the North American eusirid species total, and is nearly double the number (8) recorded to date from the Asiatic Pacific coast. Many of these North American species are regionally endemic, some newly described (above). Furthermore, in the eastern North Pacific, benthic species of *Rhachotropis* extend well down the coast, from Alaska to Baja California, whereas in the western North Pacific, the six sublittoral coastal species penetrate from the arctic to the Bering Sea and Sea of Okhotsk, barely reaching the northern Sea of Japan, and none are considered endemic.

Phyletically, *Rhachotropis* is here concluded to be the morphologically most advanced of the 13 described genera within family Eusiridae. *Rhachotropis* is autapomorphic in several character states (e.g. the shortened segment 4 of peraeopods 3 and 4) and stands apart from the other genera. On the other hand, the body form, size relationships of the posterior peraeopods (subequal peraeopods 5 and 6 and elongate peraeopod 7) and lanceolate uropods, renders the primitive "*aculeata*" subgroup of possible ancestral "outgroup" significance to the Oedicerotidae. The latter family comprises regional counterpart carnivorous amphipods that burrow into soft bottom sediments, from the shoreline to the abyss. Within the genus *Rhachotropis*, both the most primitive and most advanced species are found among the North American complex of species (Fig. 34, p. 51). By contrast, few but the most primitive species of *Rhachotropis* occur on the Asiatic Pacific coast.

We might tentatively conclude, therefore, that the North Pacific region represents a major centre of origin and evolution of eusirid amphipods in general, and the North American Pacific sub region represents a major centre of evolution within the advanced genus *Rhachotropis*. Within *Rhachotropis*, evolutionary thrust appears to have involved morphological reductions on the one hand (e.g. loss of pigmented eyes, body armature, and decrease in body size) and functional specializations on the other (e.g. elongation of appendages and dactyls) for penetration and exploitation of food resources of both epibenthic abyssal, and meso- and abyssal pelagic marine niches.

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TABLE IV. Collection Abbreviations

ELB = senior author
 EAH = junior author
 KEC = K. E. Conlan, CMN, Ottawa, Canada
 PS = Peter Slattery, Moss Landing, California
 IOS = Institute of Ocean Sciences, Sidney, B. C.
 CMN = Canadian Museum of Nature, Ottawa, Canada
 GWO = G. W. O'Connell
 JLB = J. L. Barnard (deceased)
 NMCD = Neil McDaniel, Vancouver, B. C.
 NMNS = National Museum of Natural Sciences, Ottawa.
 OSU = Oregon State University
 PF = Peter Frank, CMN, Ottawa.
 RBCM = Royal British Columbia Museum, Victoria, B. C.
 USNM = U. S. National Museum (Natural History)

TABLE V. Abbreviations in figures

A1 - antenna 1	MX1 - maxilla 1
A2 - antenna 2	MX2 - maxilla 2
AC. FL. - accessory flagellum	O. P. - outer plate
CIC -- calceolus	P3-P7 - peraeopods 3-7
CX - coxa	PER - peraeon
DCTL - dactyl	PL1-3 - pleopods 1-3
EP1-3 - pleon plates 1-3	PLEOS - pleosome
GN1 - gnathopod 1	PLP - palp
GN2 - gnathopod 2	RT - right
I. P. - inner plate	T - telson
LFT - left	U1-3 - uropods 1-3
LL - lower lip	UL - upper lip
MD - mandible	UROS - urosome
	MXPd - maxilliped
	ov. - ovigerous

APPENDIX.

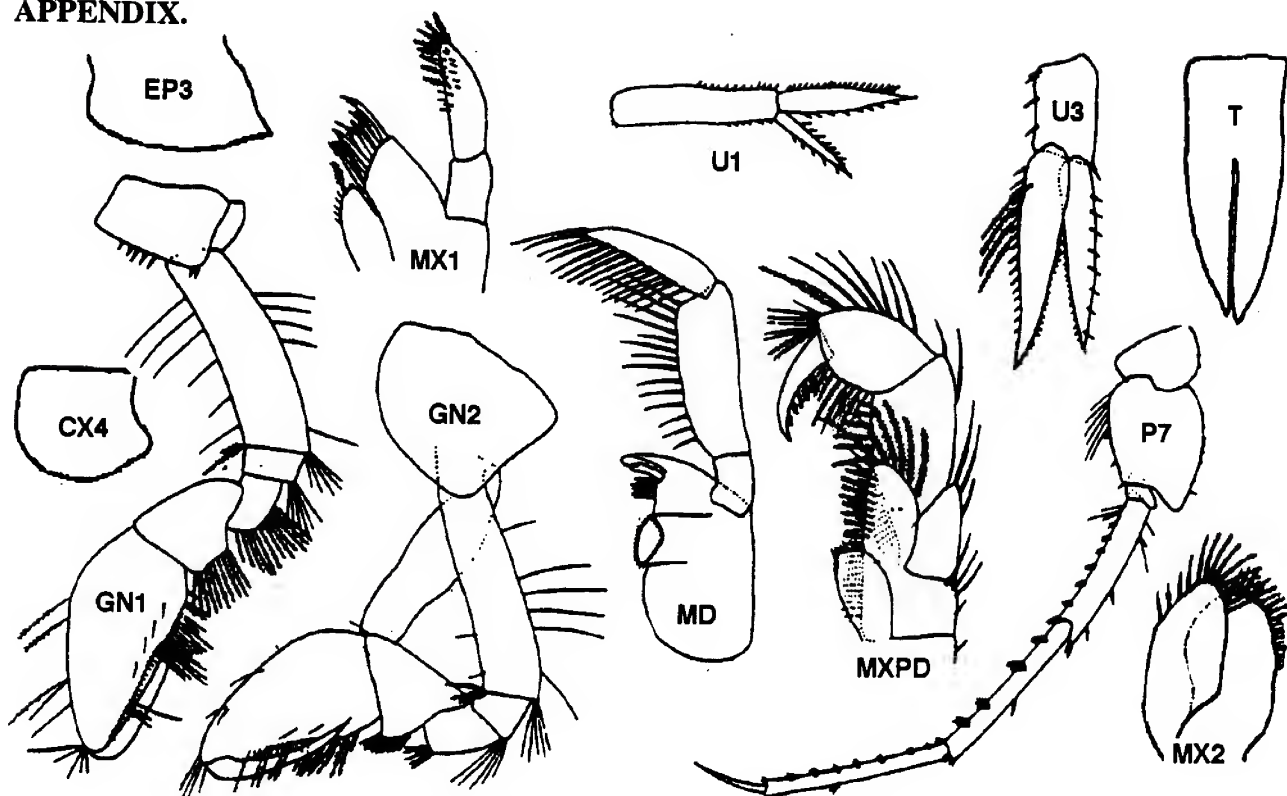


FIG. 35. *Harcledo curvidactyla* (Pirlot, 1929). Female ov. (21 mm)
Kurile-Kamchatka Trench. (modified from Birstein & Vinogradov, 1955)

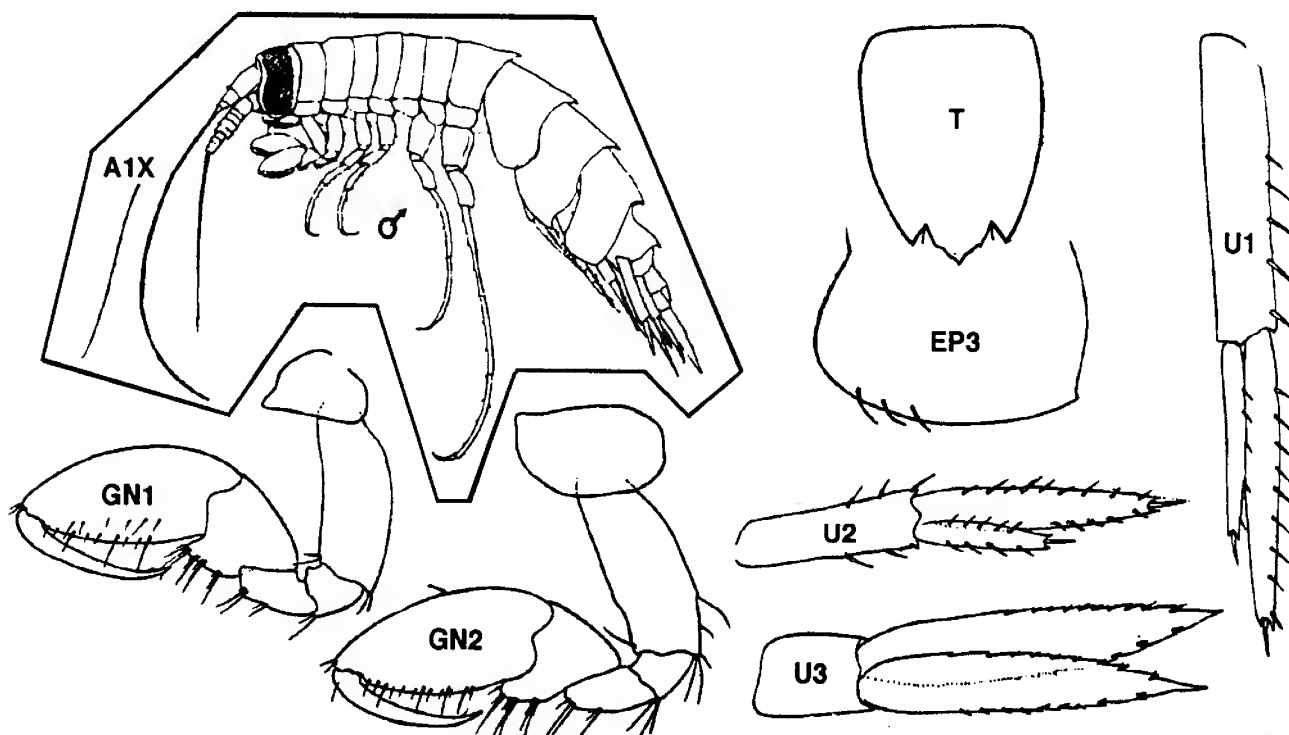


FIG. 36. *Stenopleura atlantica* Stebbing, 1888. Northwestern Pacific (0-600 m tow)
Male (7.5 mm). (after Birstein & Vinogradov, 1960)

INSET: *Stenopleuroides macrops* Birstein & Vinogradov, 1964) Indian Ocean.

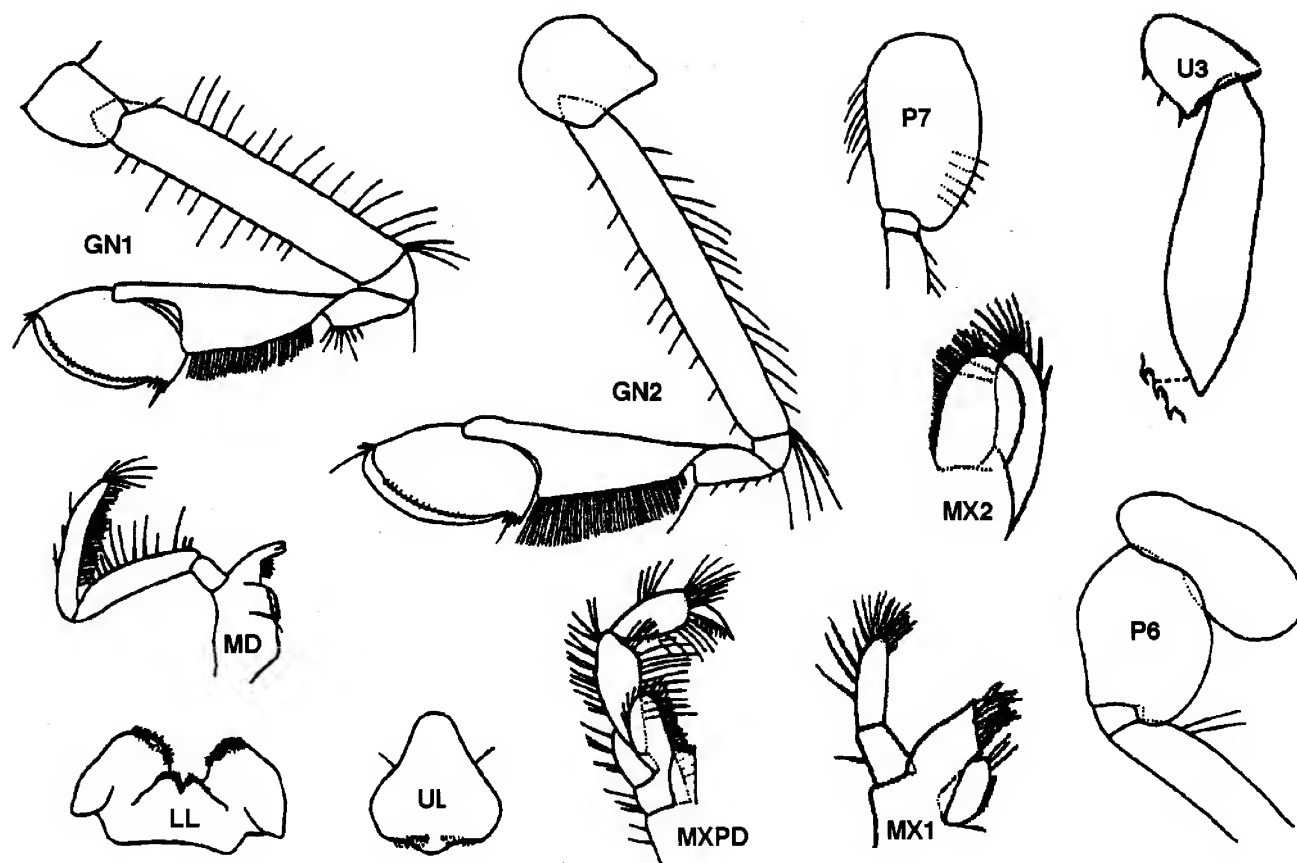


FIG. 37. *Pareusirogenes carinatus* Birstein & Vinogradov, 1955. Female (19.0 mm)
Kurile-Kamchatka Trench (modified from B. & V. 1955)

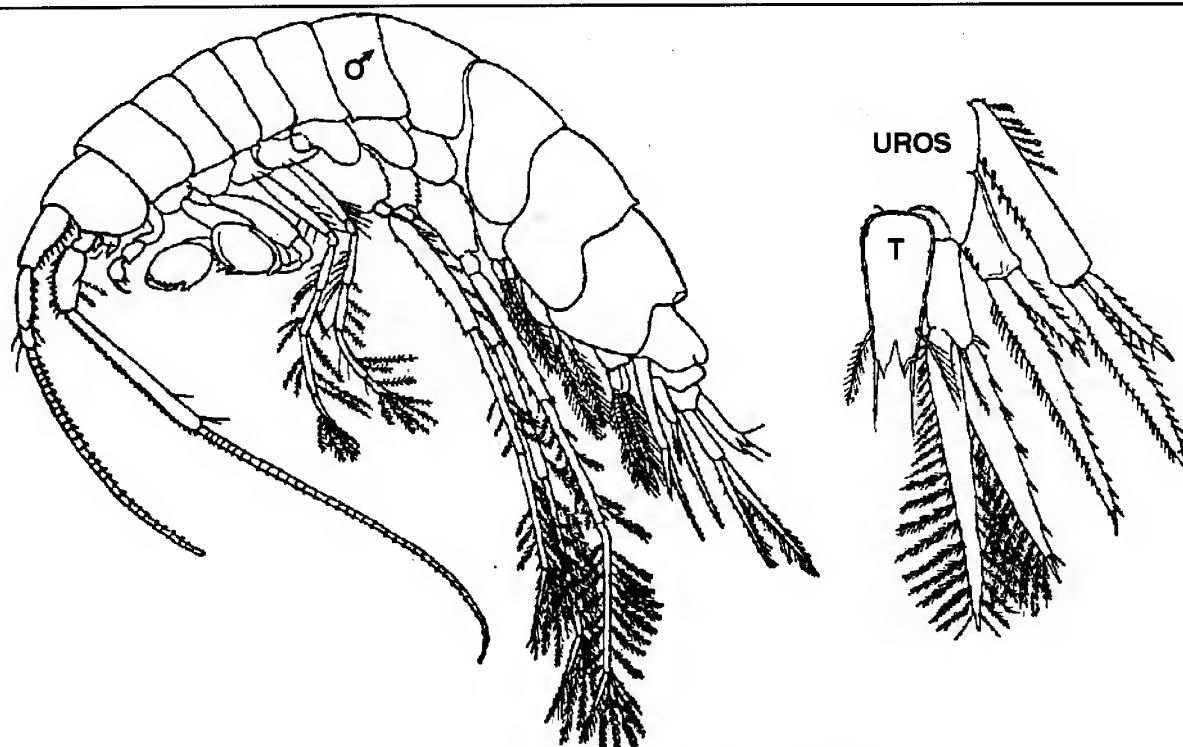


FIG. 38. *Eusiropsis riisei* Stebbing, 1897. Male (10.0 mm)
North Atlantic Ridge (modified from Stebbing, 1906)

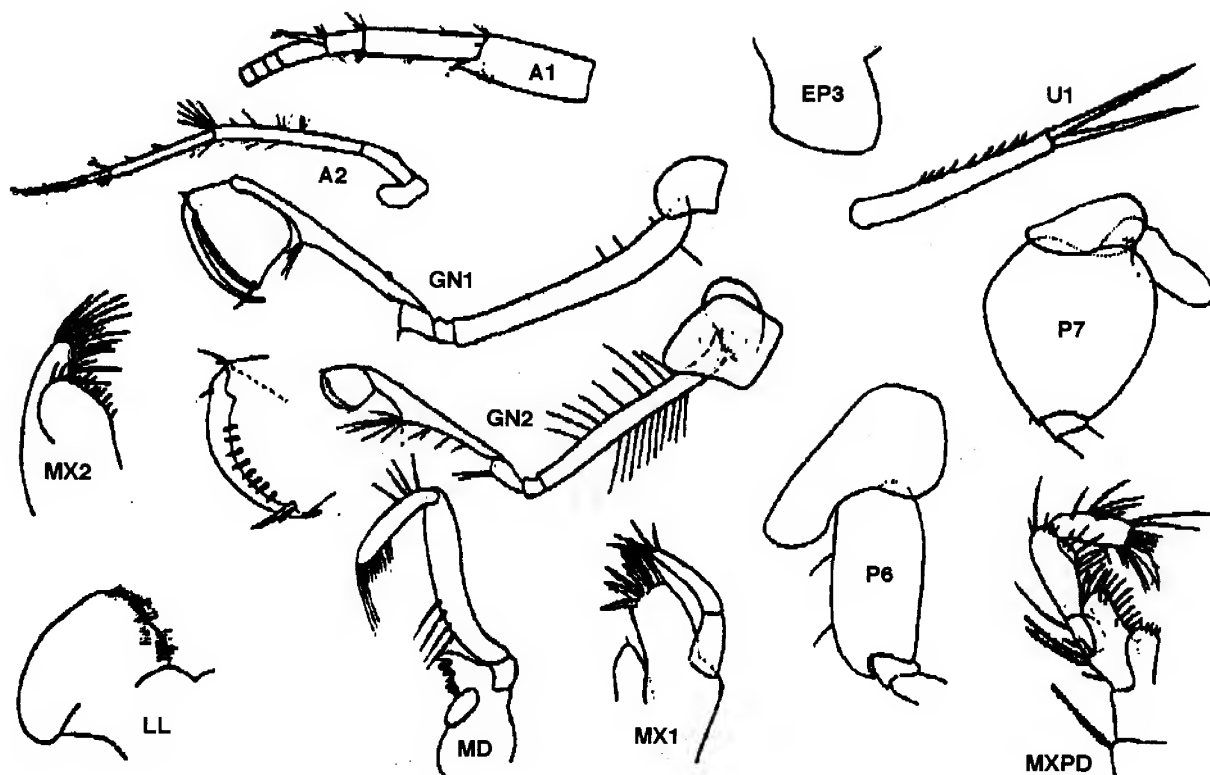


FIG. 36. *Eusirogenes homocarpus* Birstein & Vinogradov, 1955. Kurile-Kamchatka Trench (modified from B. & V., 1955)

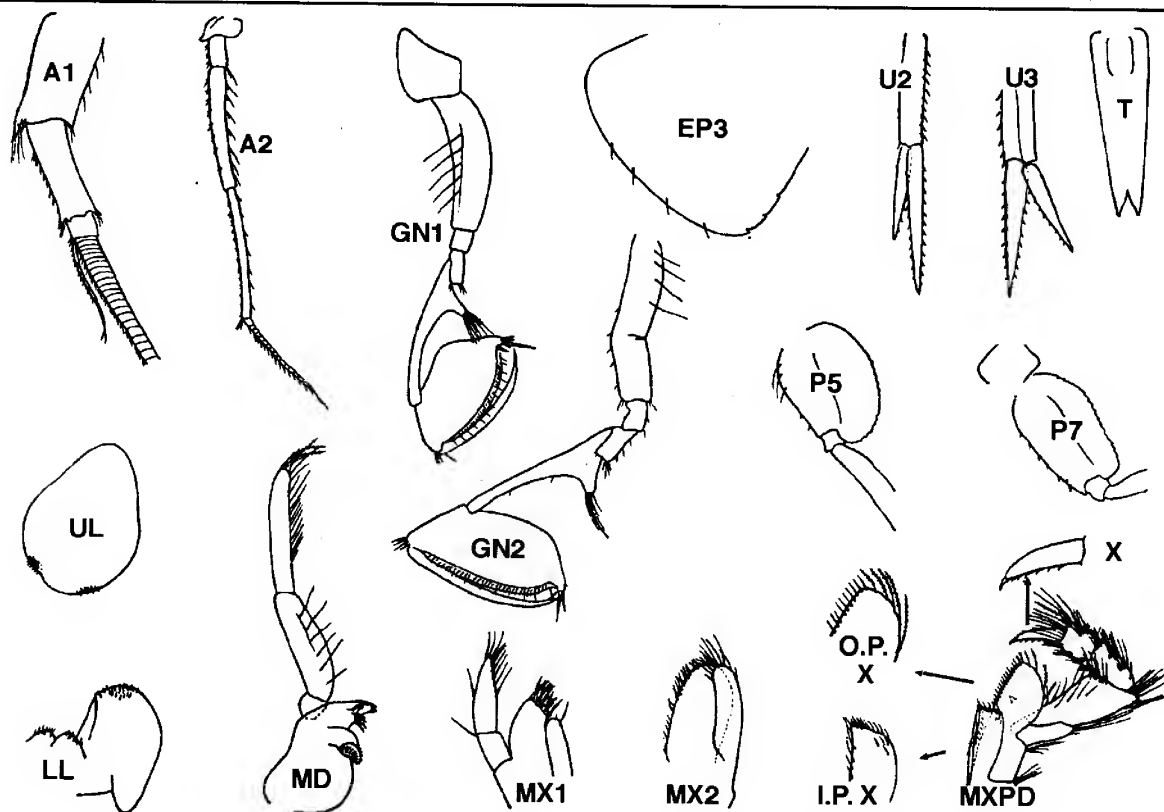


FIG. 40. *Eusirus bathybius* Schellenberg, 1955. Male? (17.0 mm)
N. Pacific, off Japan, 0-7500 m (modified from Birstein & Vinogradov, 1960)

The Canadian Field-Naturalist

**A continuation of 115 years of publication on northern North American
biodiversity — 1880-1994**

The Canadian Field-Naturalist is the official publication of The Ottawa Field-Naturalists' Club and features both articles and notes on original research and observations on the natural history of northern North America (including distribution, faunal analyses, taxonomy, ecology, and behaviour). Issues include news and comment (Club annual meetings and awards, tributes and review papers) and book review and new title sections. Since 1984, it has presented edited Status Reports for individual species designated by the Convention on Species of Endangered Wildlife in Canada (COSEWIC). It is entirely supported through club membership and subscriptions, page and reprint charges. The Ottawa Field-Naturalists' Club has 1041 members and *The Canadian Field-Naturalist* an additional 248 individual and 573 institutional subscribers, for a distribution of 1862 copies.

The Ottawa Field-Naturalists' Club was formed in 1879 by scientists from embryonic federal departments including the Geological Survey and the Dominion Experimental Farm and leading amateurs; this type of mix remains its strength to this day. The Club quickly emphasized publication, and for seven years beginning in 1880, it annually issued the *Transactions of the Ottawa Field-Naturalists' Club*. With volume 3 in 1887, the *Transactions* became a subtitle of Volume 1 of *The Ottawa Naturalist*, a monthly publication. With Volume 3 of *The Ottawa Naturalist* in 1889 the emphasis changed from local members reports to national ones, and in 1919 the journal was renamed *The Canadian Field-Naturalist* (starting with Volume 33 which was Volume 35 of the *Transactions* but this subtitle was subsequently dropped). The issues per year were gradually reduced from 12 to 9 to 6 and eventually to 4, the latter beginning with Volume 67 in 1953. However, the annual number of pages increased, in 1988 (volume 102) reaching a record of 798 with a the largest single issue of 216 pages in 102(2). Since 1967, the Club has separately published a local (Ottawa area) natural history journal, *Trail & Landscape*, now also issued 4 times a year.

Submissions to *The Canadian Field-Naturalist* and predecessors have long been peer reviewed, first through a "Publishing Committee", later "Sub-editors", and then "Assistant Editors" until the designation "Associate Editors" was adopted in 1885 and maintained ever since. Currently, most submissions also go to at least one (and often more) additional reviewer(s). Associate Editors are listed in every issue and since 1982 additional reviewers been acknowledged annually in the Editor's Report. A formal publication policy was published in *The Canadian Field-Naturalist* 97(2): 231-234. "Advice to Contributors" is published in one or more issues annually. The current subscription rate is \$23 for individuals and \$38 for institutions. Postage outside Canada is \$5.00 additional. Subscriptions should be sent to The Canadian Field-Naturalist, Box 35069 Westgate P.O., Ottawa, Ontario, Canada K1Z 1A2. Manuscripts for consideration should be addressed to Dr. Francis R. Cook, Editor, Canadian Field-Naturalist, RR 3, North Augusta, Ontario, Canada K0G 1R0.

Francis R. Cook

THE AMPHIPOD GENUS *PARAMOERA* MIERS (GAMMARIDEA: EUSIROIDEA: PONTOGENEIIDAE) IN THE EASTERN NORTH PACIFIC

Craig P. Staude¹

ABSTRACT

Six new species and one subspecies of the amphipod genus *Paramoera* are described from the eastern North Pacific, bringing the total to 12 congeneric species in this region. *Paramoera serrata*, new species, *P. serrata escofetiae*, new subspecies, *P. suchaneki*, new species, and *P. bousfieldi*, new species, form the unresolved grade "*Paramoera*" with the type species *P. australis* Miers, 1875 and most other *Paramoera* of the Southern Hemisphere. The new subgenus *Moanamoera* is erected to receive the three Hawaiian species previously described by J. L. Barnard (1977). *Paramoera leucophthalma*, new species and *P. crassicauda*, new species, are placed in the new subgenus *Humilomoera*. *Rhithromoera*, new subgenus, is erected to receive *Paramoera carlottensis* Bousfield, 1958 and *P. bucki*, new species. Members of these more advanced subgenera of the North Pacific exhibit some reduction in morphological characters and are found mostly in waters of reduced salinity. A regional key to species is presented, and distributional and ecological information is given for each species. The systematic relationship among the regional species is contrasted with the marine congeners of the Southern Hemisphere. Evolutionary and biogeographic trends are discussed.

INTRODUCTION

Amphipods of the genus *Paramoera* are common inhabitants of marine cobble and gravel beaches along the western coast of North America. Some species are estuarine, entering the tidal portion of streams. They attain high population densities and provide a significant prey resource to fishes (Staude, 1986). Yet despite their importance, these amphipods are poorly known.

Our first knowledge of the amphipod genus *Paramoera* was prompted by an international expedition to observe the transit of Venus in 1874 and 1875. The United States, Germany, and Great Britain each established astronomical observatories on the remote southern island of Kerguelen. The Rev. A. E. Eaton, naturalist of the British expedition, collected numerous specimens of flora and fauna from the area, including those destined to become the type specimens of *Paramoera*.

Miers (1875a) formally described these specimens as *Paramoera australis*, and diagnosed the genus on the basis of four characters: antenna 1 being slightly longer than antenna 2, gnathopods being subequal and well developed, uropod 3 ("posterior pleopoda") having a rudimentary inner ramus, and the telson being cleft nearly to its base.

The inadequacy of this description soon became apparent. One month later, Miers (1875b) attempted to retract his original designation. He moved *australis* to the genus *Atylus*, admitting that he had been mistaken about the condition of uropod 3. He further suggested (Miers, 1879) that a new

genus be erected to receive *Atylus australis* as well as *Amphitoe fissicauda* of Dana (1852) and *Atylus austrinus* of Bate (1862), but he did not formally establish such a genus. This new group lacked the dorsal carinations of *Atylus*, and was grossly similar to the genus *Melita*, but lacked an obvious accessory flagellum.

Miers (1879) still entertained the thought that his genus name of *Paramoera* could be applied to species with reduced uropods, but by 1885 he had become resigned to its demise. In a letter cited by Stebbing (1888) Miers commented, "I suppose the genus *Paramoera* will hardly stand."

Stebbing's report on the Challenger Expedition (1888) decreed *Paramoera* to be "scientifically unsuitable" and unrevivable due to the inaccuracies of the original diagnosis. He erected the genus *Atylodes* to receive the orphaned species, *Paramoera australis*. But eighteen years later Stebbing reversed his decision. In his authoritative monograph of 1906 Stebbing reestablished the name *Paramoera*, and provided a revised diagnosis. Yet in that same work he synonymized and submerged the type species, *Paramoera australis* Miers, with *P. austrina* (Bate). Under the present rules of nomenclature, *P. australis* Miers 1875 remains the legitimate type species of the genus *Paramoera* (confirmed by Dr. Melville of the International Commission of Zoological Nomenclature via personal communication with Dr. M. Thurston, 1985).

Another blow was dealt by Schellenberg in 1931 who synonymized twenty taxa of earlier authors under the name *Paramoera fissicauda* (Dana). Most of these sweeping changes were reversed by later authors (K.H. Barnard, 1932; Thurston, 1972; Bellan-Santini and Ledoyer, 1974).

¹Friday Harbor Laboratories, University of Washington, Friday Harbor, WA, 98250, USA

This shuffling of nomenclature and the inadequacy of most early descriptions have left this group in a crippling state of confusion. While working on subantarctic species of *Paramoera*, J.L. Barnard (1972a) complained, "I am yet unable to turn to the literature and easily make some sense of the species without painstaking cross-referencing that often terminates blindly." He rediagnosed the genus (J.L. Barnard, 1972b), but concluded that "the identity of various species of *Paramoera* is so confounded presently that I cannot properly evaluate variables within that genus." Bellan-Santini and Ledoyer (1974), in their comprehensive review of *Paramoera*, concurred that a revision is necessary.

Throughout this century the number of species of *Paramoera* has grown to more than forty. Marine and freshwater species were discovered in the vicinity of Japan and Korea (Tattersall, 1922; Stephensen, 1944; Bulychcheva, 1952; Ueno, 1933, 1971a, 1971b), and three species were reported from the Pacific coast of North America (J.L. Barnard, 1952; Bousfield, 1958). When J.L. Barnard added three unusual new species from Hawaii in 1977 he suggested that they might qualify as a new subgenus of *Paramoera*, but he hesitated to erect this taxon because of the "taxonomic instability" of many pontogeneiid genera.

In 1982 J.L. Barnard and G.S. Karaman began to carve up this unwieldy composite of species into new allied genera. Japanese species with sinusoid cephalic lobes were assigned to *Relictomoera*, while those with sternal gills became *Sternomoera*. But even this recent revision is problematic. Hirayama (1990) has urged the submergence of the genus *Relictomoera*, claiming that the cephalic lobes of these species are not unusual for the genus *Paramoera*. The need is apparent for further investigation of these western North Pacific species at the level of genus or subgenus.

A major impediment to the resolution of *Paramoera* (*sensu lato*) is our incomplete knowledge of the type specimens. Miers' original description (1875a) and his further elaboration in 1879 fail to provide an adequate basis for comparison of the many species which have since been discovered around the world. In 1974 Thurston urged the reexamination of this and other early species. He has since succeeded in resurrecting Mier's specimens which were entombed in the British Museum, and has begun to redescribe and refigure both *Paramoera australis* and *P. austrina* (Thurston, pers. comm.). The final disposition of *Paramoera* and its allied genera will depend on further developments in this area.

Until recently (Staude 1987), only 3 species of *Paramoera* were recognized in the eastern North Pacific (Bousfield 1958, Barnard, 1975). The environmental concern of the last three decades prompted numerous baseline surveys of marine invertebrates (e.g., Armstrong et al., 1976; Nyblade, 1979), uncovering additional species. A closer examination of museum collections has revealed still other undescribed species of *Paramoera*.

This paper formally describes 6 new species (and one new subspecies) of *Paramoera* from the west coast of North America, making a total of 9 for this region and 3 from the

adjacent Hawaiian Islands. These new discoveries suggest three or more subgeneric groups.

METHODS

The material examined in this study was collected from 45 geographic localities from the Pribilof Islands to Ensenada, Mexico, and was made available from numerous sources.

The names of collectors or the institutions where material is housed are abbreviated as defined in Table 1.

TABLE 1. Collection abbreviations

AE = Anamaria Escofet, Centro de Invest. Cientificas, Ensenada, Baja California, Mexico
AHF = Allan Hancock Foundation, Los Angeles, CA (now at the L.A. County Museum)
AR = Anthony Roth, Nautilus Associates, Port Angeles, WA
BM = Dr. Bruce Miller, University of Washington
CAS = California Acad. of Sciences, San Francisco, CA
CFN = Dr. Carl F. Nyblade, University of Washington
CPS = author
CL = Dr. Colin Levings, Pacific Environmental Inst., Vancouver, BC
CS = Charles A. Simenstad, University of Washington
ELB = Dr. E.L. Bousfield, National Museums of Canada
FGH = Dr. F. G. Howarth, Bishop Museum, Hawaii
FR = Fahmida Rafi, National Museums of Canada
G and S = Ghelardi and Sikora, University of California
JDC = John D. Chapman, University of California
JLB = Dr. J.L. Barnard, U.S. National Museum
JLM = Dr. John L. Mohr, Univ. of Southern California
JTC = Dr. John T. Carlton, California Acad. of Sciences
JWA = Dr. John W. Armstrong, Univ. of Washington
LACM = Natural Hist. Museum of Los Angeles County
METRO = Municipality of Metropolitan Seattle, WA
MLM = Dr. Michael L. Murphy, Nat'l. Marine Fish. Service, Auke Bay, AK
NMC = National Museums of Canada (now Canadian Museum of Nature)
NOAA = National Oceanic and Atmos. Admin. (Puget Sound MESA Program)
PS = Mr. Patrick Shaw, Univ. of British Columbia
PNS = Dr. Peter N. Slattery, Moss Landing Lab., CA
RJL = Ronald J. Long, Simon Fraser University, Vancouver, BC
RJM = Dr. Robert J. Menzies, Univ. of Southern Calif.
SAM = South African Museum
SJS = Sarah J. Staude, author's assistant
THS = Dr. Thomas H. Suchanek, Univ. of Washington
USNM = U. S. National Museum (Natural History)

The major portion of the loan material was borrowed from the National Museum of Natural Sciences, National Museums of Canada. Collection information for these specimens was reported by Bousfield (1957 and 1963),

Bousfield and Hubbard (1968), and Bousfield and Jarrett (1981).

Many specimens were personally (Staude, 1986) collected by means of live (350 μ m) and dead (500 μ m) sieving of sediment cores, by 0.3 m hand-towed plankton net (330 μ m mesh), and by a suction sampler or coarse forceps. Qualitative samples were also taken by a "bucket swirl" technique, in which small amounts of sediment were agitated in a bucket of clean seawater, the bucket swirled, and the water decanted through a sieve. Scuba collections of sediment cores were made at Cape Beale, B.C., and at Deadman Bay, Washington.

Specimens of the author's collection were fixed in 10% buffered formalin, and preserved in 70% ethanol with 5% glycerol. Selected specimens were stained with lignin pink or methylene blue, dissected in a glycerol/ethanol (1:1) solution and mounted in 96% glycerol with a ringed coverslip. Illustrations were made by camera lucida with both dissecting and compound microscopes. The specimens were optically "uncurled" and body parts optically repositioned to provide a uniform figure. Body length was measured from the tip of the rostrum to the base of the telson.

Abbreviations of illustrations are defined in Table 2.

TABLE 2. Abbreviations used in figures

A1 = antenna 1	MX1 = maxilla 1
A2 = antenna 2	MX2 = maxilla 2
C2 = coxa 2	MXPD = maxilliped
EP3 = epimeron 3	PL2 = pleopod 2
GC = gland cone	P4 = peraeopod 4
GN1 = gnathopod 1	P7,2 = P7, segment 2
GN2 = gnathopod 2	RT = right
LFT = left	U1 = uropod 1
LL = lower lip	U2 = uropod 2
LM = lacinia mobilis	U3 = uropod 3
m = male	T = telson
MD = mandible	

The information presented here is condensed from a more rigorous examination contained in my dissertation (Staude, 1986). That work includes full descriptions of female holotypes and male paratypes for each new species, and contains the detailed phenetic and cladistic analyses on which I base the new subgenera. The phenetic clustering was performed using the CLUSTAN program at the University of Washington Academic Computing Center utilizing the group averaging method (Sneath and Sokal, 1973). The cladistic analysis was done on a microcomputer using various routines of the program PHYLIP (Felsenstein, 1984, 1985). The fifty-two characters used in these analyses were presented in my dissertation (Staude, 1986). For the purpose of these phyletic comparisons, the group ancestor was in part patterned after *Paramoera bidentata* K.H. Barnard, 1932, and the "type" concept was based on personal communication and

unpublished materials from Dr. Michael Thurston, who has reexamined the type material of the genus *Paramoera*.

Throughout this paper there are references to a publication in press (e.g., "*Paramoera serrata* Staude (in press)") that were originally cited (Staude, 1987) in an identification guide to invertebrates (Kozloff, 1987). Unfortunately, that paper never appeared in print due to funding cuts and policy changes at the supporting institution.

SYSTEMATICS

Paramoera Miers, 1875

Paramoera Miers, 1875a: 75.--Stebbing, 1906: 363.--Schellenberg, 1929: 280.--J. L. Barnard, 1969a: 227.--Barnard, 1972b: 184-186.--Barnard, 1977: 275-278.

Stebbingia Pfeffer, 1888 (fide J. L. Barnard, 1969a)

Atyloides Stebbing, 1888.

Aucklandia Walker, 1908 (fide J. L. Barnard, 1969a)

Type species. *Paramoera australis* Miers, 1875.

Diagnosis. Rostrum vestigial or absent; antenna 1 usually longer than antenna 2; accessory flagellum 1-segmented, scale-like, with 2 long apical setae and a shorter seta to either side; gland cone projecting ventrally, bearing spines or setae; discoid calceoli present in male.

Upper lip symmetrical and evenly rounded; mandibular incisor with 6 teeth, left lacinia mobilis with 5 teeth, right lacinia with 2-3 major teeth, with a blunt tooth at the base of the mandibular palp; segments 2 and 3 of mandibular palp subequal in length; lower lip with inner lobes indistinct or absent; inner plates of maxilla 1 and 2 generally with numerous plumose setae (reduced in apomorphic subgenera), setae of maxilla 2 in a submarginal diagonal row; inner plate of maxilliped with 3 stout apical spine teeth.

Coxae 1-4 without articulated spines along the posterior margins; gnathopods subchelate (not eusirid), with oblique palms, propodus with groups of finely pectinate comb-setae in parallel arrangements along the ventral, medial, and anteromedial margins; carpus of gnathopod 2 lengthened in female (often exceeding the length of the propodus).

Lobes of telson rarely fused more than half its length, with prominent setae or spines near the apices.

Relationships. *Paramoera* differs from *Accedomoera* J. L. Barnard (1964) in the smaller rostrum, the ornamentation of the accessory flagellum, the absence of distinct inner lobes on the lower lip, the more setose maxillae, the absence of spines along the posterior margins of coxae 1-3, the more uniform alignment of gnathopod setae, and the ornamentation of the apices of the telson. It differs from *Pontogeneia* Boeck (1871) by the shorter rostrum, the presence of an accessory flagellum, the ventrally extended (ornamented) gland cone, the longer article 3 of the mandibular palp, the absence of distinct inner lobes on the lower lip, the more setose maxillae

(exceptional subgenera), the absence of spines from the posterior margins of coxae 1-3, the more uniform alignment of the gnathopod setae, and the ornamentation of the apices of the telson. Differing from *Gondogeneia* J. L. Barnard (1972b) by the shorter rostrum, the longer antenna 1, the ventrally extended (ornamented) gland cone, the broader and more setose inner plate of maxilla 1, the greater setosity of maxilla 2 (exceptional subgenera), the more uniform alignment of the gnathopod setae, and the longer basal segments of pereopods 5-7. Differing from *Tethygeneia* J. L. Barnard (1972b) by the shorter rostrum, the structure of the accessory flagellum, the ventrally extended gland cone, the longer segment 3 of the mandibular palp, the more slender palp of maxilla 1, the more setose maxillae (exceptional subgenera), the more uniform alignment of the gnathopod setae, and by the ornamentation of the apices of the telson. Differing from *Nasageneia* Barnard & Karaman (1982) by the shorter rostrum, the presence of an accessory flagellum, the ventrally extended gland cone, the longer segment 3 of the mandibular palp, the less serrate epimeron 3, and the ornamentation of the apices of the telson. Differing from *Pontogeneiella* Schellenberg (1929) by the shorter rostrum, the presence of an accessory flagellum, the ventrally extended gland cone, the absence of inner lobes from the lower lips, the absence of spines from the posterior margin of coxae 1-3, and the lesser fusion of the telson lobes. Differing from *Antarctogeneia* Thurston (1974) by the presence of an accessory flagellum, the longer segment 3 of the mandibular palp, the absence of inner lobes from the lower lip, the unexpanded coxa 1, the structure of the pereopod dactyls,

and the less serrate epimeron 3. Differing from *Atyoella* Schellenberg (1929) by the unproduced epistome and the absence of inner lobes from the lower lip. Differing from *Atyopsis* Stebbing (1888) by the absence of inner lobes from the lower lip, the more setose maxillae, and the lesser fusion of the telson lobes. Differing from *Schraderia* Pfeffer (1888) by the more robust (non-linear) gnathopods and the less serrate epimera. Differing from *Apherusa* Walker (1891) by the longer first antenna, the presence of an accessory flagellum, and the presence of calceoli in the male. Differing from *Djerboa* Chevreux (1906) by the more robust (non-linear) gnathopods and the absence of an accessory spine from the dactyls of the pereopods. Differing from *Awacaris* Ueno (1971c) by the presence of eyes, the more typical mandibular incisor, the typical (unreduced) palp of maxilla 1, and the more uniform ornamentation of uropod 3.

Component groups

The genus *Paramoera* encompasses the grade "*Paramoera*" (the type specimen and its closest relatives, including subgenera that are presently unresolved) and the subgenera *P. (Moanamoera)*, new subgenus, *P. (Humilomoera)* new subgenus, and *P. (Rhithromoera)*, new subgenus.

The diagnosis and composition of this genus are provisional. Subsequent revision of antiboreal species (including the type species) will provide further resolution. The genera *Paramoerella* Ruffo (1974), *Pseudomoera* Schellenberg (1929), *Relictomoera* Barnard & Karaman (1982; see also Hirayama 1990), and *Sternomoera* Barnard & Karaman (1982) are candidates for future designation as subgenera.

Key to *Paramoera* of the eastern North Pacific (adults of both sexes)

1. Head with an acute notch or cleft (inferior antennal sinus) separating the lateral lobe and post-antennal lobe; eye larger than 1/2 the depth of the lateral lobe of the head 2.
- Head with a smoothly curved or quadrate concavity separating the lateral lobe and postantennal lobe; eye not larger than 1/2 the depth of the lateral lobe 7.
2. Head with a slight cleft separating the lateral lobe and postantennal lobe; gland cone with a single short seta; gnathopod 2 of female with carpus more than 25% longer than propodus; uropod 3 without plumose setae *Paramoera (Paramoera) bousfieldi* (p. 78)
- Head with a moderate to deep notch or cleft separating the lateral lobe and postantennal lobe; gland cone with 1-4 long setae or with stout spines; gnathopod 2 of female with carpus not more than 25% longer than propodus; uropod 3 with plumose setae (these sometimes reduced and hidden in lateral view) 3.
3. Gland cone with 1-2 stout spines (plus a seta in female); segment 3 of antenna 2 with dorso-distal spine; segment 6 of pereopod 4 with posterior row of spines in groups of 2-3; inner ramus of uropod 2 with subapical spine larger than proximal spines *P. (P.) columbiana* (p. 77)

- Gland cone with setae only; segment 3 of antenna 2 without a distodorsal spine; segment 6 of peraeopod 4 with a posterior row of single spines (+ small setae); inner ramus of uropod 2 with subapical spine not larger than proximal spines 4.
4. Segment 6 of peraeopod 4 with more than 4 spines in the posterior row; posterior margin of epimeron 3 with more than 3 small posterior notches; outer ramus of uropod 2 longer than inner ramus. *P. (P.) suchaneki* (p. 73)
- Segment 6 of peraeopod 4 with not more than 4 spines in the posterior row; posterior margin of epimeron 3 with 2 small notches; outer ramus of uropod 2 shorter than inner ramus 5.
5. Head with a shallow cleft separating the lateral lobe and postantennal lobe; segments 1 and 2 of antenna 1 with about 4 groups of long setae along the ventral margins; gland cone of antenna 2 with one long and one short seta *P. (P.) mohri* (p. 68)
- Head with a deep cleft separating the lateral lobe and postantennal lobe; segments 1 and 2 of antenna 1 with 5 or more groups of long setae along the ventral margins; gland cone of antenna 2 with 4-6 long setae. 6.
6. Segment 6 of peraeopod 4 with 3 spines in the posterior row; segment 2 of peraeopod 7 with distinct posterior serration; urosomite 3 with a distinct dorsal boss (Washington to central California). *P. (P.) serrata* (p. 69)
- Segment 6 of peraeopod 4 with 5 spines in the posterior row; segment 2 of peraeopod 7 without obvious posterior serration; urosomite 3 without a distinct dorsal boss (Baja California). *P. (P.) serrata escofetae* (p. 70)
7. Antenna 1 much longer than antenna 2; inner plate of maxilla 1 with about 4 plumose setae; epimeron 2 with posteroventral corner quadrate or obtusely angled; uropod 3 without plumose setae (Alaska to Washington) 8.
- Antenna 1 not much longer than antenna 2; inner plate of maxilla with about 10 plumose setae; epimeron 2 with posteroventral corner acutely angled; uropod 3 with plumose setae (Hawaiian Islands) (*Moanamoera*, n. s.-g.) 11.
8. Head with a deep concavity (inferior antennal sinus) between the lateral lobe and postantennal lobe; gland cone with 1-2 crooked spines; propodus of gnathopods about twice as long as wide; gnathopod 2 of female with carpus shorter than propodus; peraeopods 5-7 with carpus slightly longer than propodus; each apex of telson with 3-4 setae (*Rhithromoera*, n. s.-g.) 9.

- Head with a shallow concavity (inferior antennal sinus) between the lateral lobe and postantennal lobe; gland cone with a single small seta; propodus of gnathopods more than twice as long as wide; gnathopod 2 of female with carpus not shorter than propodus; peraeopods 5-7 with carpus shorter than propodus; each apex of telson with less than 3 setae . . . (*Humilomoera*, n. s.-g.) 10.
9. Eye about 1/3 the depth of the lateral lobe of head; propodus of gnathopods widest proximal to their midpoint; gills absent from peraeopod 7; peduncle of uropod 1 with more than 10 spines in the dorsolateral row, and with an isolated distoventral spine. *P. (R.) bucki* (p. 91)
- Eye about half the depth of the lateral lobe; propodus of gnathopods widest at or beyond their midpoint; gills present on peraeopod 7; peduncle of uropod 1 with less than 10 spines in the dorso-lateral row, lacking an isolated distoventral spine *P. (R.) carlottensis* (p. 90)
10. Eyes light; segment 1 of antenna 1 with a distoventral spine; uropod 3 with rami much longer than peduncle; telson fused less than half its length *P. (H.) leucophthalma* (p. 84)
- Eyes dark; segment 1 of antenna 1 with setae only; uropod 3 with rami longer than the peduncle; telson fused more than half its length *P. (H.) crassicauda* (p. 84)
11. Eyes entirely absent; peraeopods elongate (combined length of segments 3-7 of peraeopod 7 more than twice the length of segment 2); uropod 3 with rami about twice the length of the peduncle (hypogean, Island of Hawaii) *P. (M.) lokowai* (p. 82)
- Eyes present (occasionally reduced to a few ommatidia); peraeopods not elongate (combined length of segments 3-7 not more than twice the length of segment 2); uropod 3 with rami less than twice the length of the peduncle 12.
12. Posterior margins of epimera with 1-3 spines; posteroventral corner of epimeron 2 produced as an acute tooth; telson fused about 25% of its length, its apices tapered and faintly notched (lava ponds, Island of Hawaii) *P. (M.) paakai* (p. 82)
- Posterior margins of epimera with 2-3 setae; posteroventral corner of epimeron 2 not produced, posterior and ventral margins meeting at about 75 degrees; telson fused only at its base, its apices broad and deeply notched (cave pools, Island of Maui) *P. (M.) rua* (p. 82)

"*Paramoera*" unresolved grade

A group of unresolved subgenera close to the form of *Paramoera australis* Miers, 1875, type species of the genus *Paramoera* Miers

Working diagnosis. Rostrum unproduced; lateral cephalic lobe mammiliform; inferior antennal sinus with a cleft. Eye large, ovate to reniform, and pigmented.

Antennae of moderate length, antenna 1 usually longer

than antenna 2, peduncular segments of antenna 1 progressively shorter, segment 1 shorter than the head; accessory flagellum 1-segmented, scale-like; ventromedial setae of peduncles long; gland cone usually with multiple setae or spines; calceoli usually present on male only.

Upper lip entire and rounded; epistome unproduced. Molar triturative, oval; palp with segments 2 and 3 subequal in length. Lower lip without distinct inner lobes.

Maxilla 1: inner plate with 8-15 plumose setae; outer plate with about 10 pectinate spines; palp long, segment 1

short. Maxilla 2: inner plate with 6-15 plumose setae in a diagonal row across the inner face. Maxilliped: inner plate about as long as outer, outer plate with more than 5 medial spine teeth; palp of 4 segments, segment 1 not laterally extended, segment 3 unlobed, segment 4 shorter than segment 3, segment 4 not spinose (but with small distal setae) along the inferior margin, ungiform, with nail.

Coxae 1-3 ordinary, a little longer than wide, sparsely setose, rarely with a developed spine or tooth at the posteroventral corner; coxa 4 with posterior lobe, excavate; anterior lobe of coxa 6 variously produced, ventral margin of coxa 6 rarely with spines (usually with setae only).

Gnathopods moderate, with subchelate oblique palm; segment 5 of gnathopod 2 rarely longer than segment 6, gnathopod 2 of males occasionally with extremely oblique palm, palm often with more than 4 barb spines in the outer row.

Dactyls of pereopods 3-7 smooth or minutely castellate, with 2 small setae near the uncinus; segment 2 of pereopods 3 and 4 not anteriorly lobate; pereopod 5 nearly as long as pereopod 7; segment 2 of pereopods 5-7 expanded and subrectangular, posteroventrally lobate; segment 5 of pereopods 5-7 shorter than segment 6. Pleopods ordinary; pleopod 2 of male often gonopodous. Posteroventral corner of epimeron 2 not acutely produced; epimeron 3 with a variable number of posterior notches, the posteroventral corner unproduced or with a small tooth.

Peduncles of uropods 1 and 2 not dorsally broadened; rami of uropod 1 subequal; outer ramus of uropod 2 usually shorter than the inner ramus. Uropod 3 extending beyond uropod 1; peduncle without a large process; rami usually equal in length, narrow, lanceolate, and usually with plumose setae.

Lobes of the telson usually fused for less than half its length, each apex usually with 2 or more setae or spines.

Long coxal gills present on pereopods 2-6 and often with a gill on pereopod 7 (although this may be reduced or absent in one or both sexes). Sternal gills absent. Female with large oostegites on pereopods 2-4 and a smaller straplike oostegite on pereopod 5; oostegite of pereopod 2 not proximally broadened, not wider than this coxa.

Relationships. "Paramoera" differs from *Paramoerella* Ruffo, 1974, by the larger eye, the cleft inferior antennal sinus, the absence of inner lobes on the lower lip, and the more fully developed gills. It differs from *Sternomoera* Barnard & Karaman, 1982, by the absence of sternal gills; and from *Pseudomoera* Schellenberg, 1929, by the more typical (non-geniculate) segment 5 of the gnathopods. "Paramoera" differs from *Moanamoera*, n. s-g., by the larger (pigmented) eye, the cleft inferior antennal sinus, the longer segment 3 of the mandibular palp, the shorter anterior coxae, the stouter gnathopods, the more rectangular segment 2 of pereopods 5-7, and the less acutely produced epimeron 2. It differs from *Rhithromoera*, n. s-g., by the larger eye, the cleft antennal sinus, the greater setosity of the antennae and maxillae, the shorter segment 1 of the maxillipedal palp, and

the shorter segment 5 of pereopods 5-7. It is also distinct from *Humilomoera*, n. s-g., in the larger eye, the cleft inferior antennal sinus, the greater setosity of the antennae and maxillae, and the more fully developed gills.

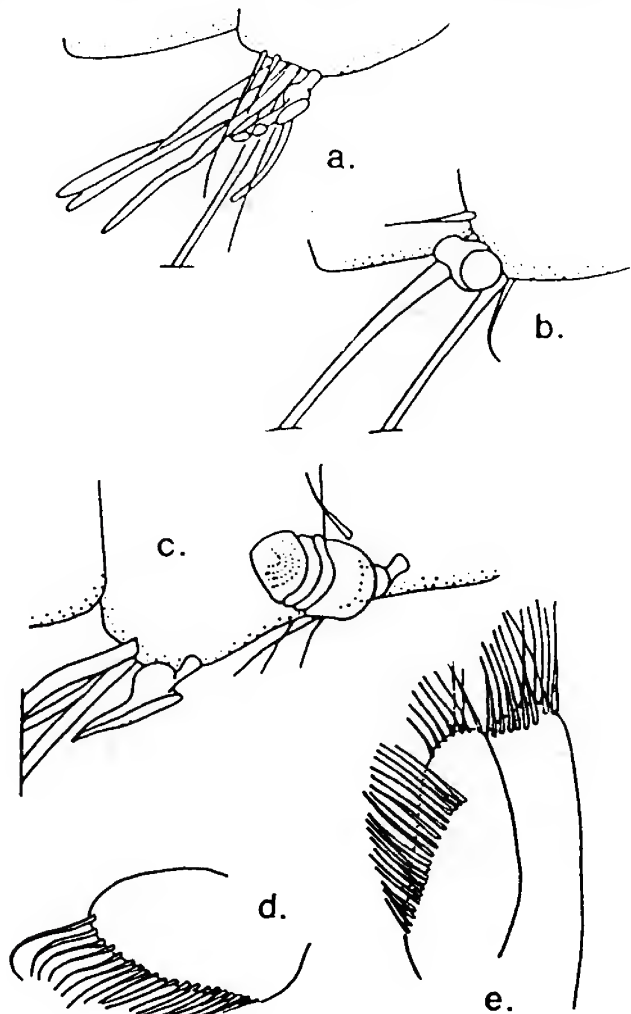


FIG. 1. Calceoli and maxillae of *Paramoera bidentata*, South Africa (SAM 1294 and SAM A12765). a. ventral setal group of a flagellar segment of antenna 1 of the female (with 3-element calceolus); b. ventral setal group of a flagellar segment of antenna 2 of the female (with key-hole shaped calceolus); c. ventral and ventromedial setal groups of the flagellum of antenna 1 of the male (with typical discoid calceoli composed of multiple elements); d. inner plate of maxilla 1; e. maxilla 2.

Component species. This grade tentatively includes all species of *Paramoera* which have not been assigned to the genera *Paramoerella*, *Relictomoera*, *Sternomoera*, or *Pseudomoera*, or to the subgenera *Moanamoera*, *Humilomoera*, or *Rhithromoera* (see Bellan-Santini and Ledoyer, 1974, and Barnard & Karaman, 1991, for comprehensive lists of species). The type species, *P. australis* Miers 1875, and its

close relative, *P. austrina* (Bate 1862), are members of this grade, although *P. austrina* apparently lacks plumose setae on uropod 3 (Thurston, pers. comm.).

The species *P. bidentata* K.H. Barnard, 1932, differs by the toothed dorsum, the more densely setose maxillae and the presence of calceoli in the female (material examined: SAM 1294 type and SAM A12765; Fig. 1). These primitive characters place *P. bidentata* close to the ancestral form of *Paramoera* and may justify its placement in a new ("protomoera") subgenus.

Paramoera walkeri (Stebbing, 1906) differs by the toothed dorsum, the reduced setosity of maxillae 1 and 2, and the fusion of its telson lobes, and may qualify as a separate subgenus. *Paramoera hurleyi* Thurston, 1972, is incongruent by its poorly setose antennae and gnathopods, the short segment 3 of the mandibular palp, and the partly fused telson. *Paramoera bousfieldi* n.sp. exhibits intermediate and advanced characters such as a faint cleft in the inferior antennal sinus, somewhat reduced setosity of maxillae 1 and 2, slender gnathopods, and a non-plumose uropod 3; linking this grade to the new apomorphic subgenera *Moanamoera*, *Humilomoera*, and *Rhithromoera*. *Paramoera capensis* (Dana, 1853) is rejected from this grade, and possibly from the entire genus *Paramoera*, on the basis of the unusual setal tufts and the absence of calceoli from the antennae of both sexes, the extreme setosity of the maxillae, the absence of medial setae on segment 6 of the gnathopods, and the foliaceous rami of uropod 3 with serrate margins (material examined: SAM 12181, SAM A3387).

This loose complex of species encompasses a wide range of habitats, usually marine, interstitial in coarse sediment or epiphytic; sub-Antarctic and holo-Pacific.

***Paramoera mohri* J. L. Barnard**
(Fig. 2)

Paramoera mohri J. L. Barnard, 1952: 16-19, pls. 3, 4;-- Barnard, 1975: 348 and 362 (in part).

not *Paramoera mohri* J. L. Barnard, 1969b: 110, fig. 15;-- Barnard, 1975: 348 and 362 (in part), pl. 73, fig. 38.

Material examined.

WASHINGTON: Deadman Bay, San Juan Island (48°30.7'N, 123°08.7'W), Staude Station A, quarterly samples of CFN and numerous samples of CPS from May 1976 to March 1986, mid- to low intertidal, gravel beach (>1000 specimens); North Beach (48°06'N, 122°47'W), April 1977, collected by CFN and AR from mid-intertidal beach of cobble over coarse sand (1 specimen); Ebey's Landing, Whidbey Island (48°11.5'N, 122°42.5'W), 26 October 1984, collected by CPS and SJS from mid- to high intertidal sandy gravel beach (2 specimens).

CALIFORNIA: Bodega Head (38°18'N, 123°03.5'W), October 1962, collected by G and S from a depth of 10 m in Horseshoe Cove (4 of >100 specimens); Bodega Head

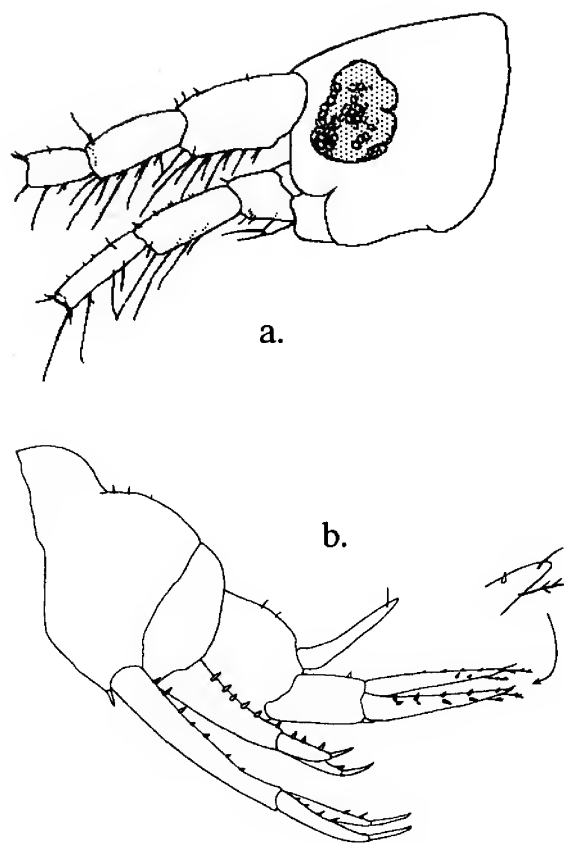


FIG. 2. *Paramoera mohri*, holotype female, 6.0 mm; Hazard Canyon Reef, California, a. head and antennal peduncles, b. urosome with detail of plumose setae.

(38°18'N, 123°03.5'W), 19 June 1982, collected by CPS from intertidal pocket of coarse gravel between uplifted rock strata (2 of >100 specimens); Carmel Point (36°32'N, 121°56'W), 18 June 1982, Staude Site 1, collected by CPS from an intertidal pool in coarse sand at the base of cobbles (1 specimen); Hazard Canyon Reef (35°17.2'N, 120°52.8'W), 2 February 1950, collected by JLM and RJM in gravel (holotype and paratypes), AHF #504; Hazard Canyon Reef, 18 September 1987, collected by CPS in gravel (12 specimens); Montana de Oro (35°15.4'N, 120°53.5'W), 1972, collected by JDC and JLC from an intertidal cave pool (3 of >100 specimens), CAS #010535.

Diagnosis. Inferior antennal sinus with a distinct cleft, postantennal lobe extended anteriorly; eye large, dark, oval (its anteroventral corner extended slightly forward); antenna 1 about 10% longer than antenna 2; major peduncular segments of antennae with about 4 groups of long setae along the ventral margins; gland cone usually with 1 long and 1 shorter seta.

Inner plate of maxilla 1 with 5-7 plumose setae; inner plate of maxilla 2 with about 5 plumose setae.

Segment 6 of gnathopod 1 with about 5 posterior groups

of comb setae; segment 6 of gnathopod 2 with 7-8 posterior groups of comb setae; gnathopod 2 of female with segment 5 about 10% longer than segment 6; gnathopod 2 of male with segment 5 about 65% as long as segment 6, segment 6 distally broadened, its palm oblique, palm about 55% as long as the posterior margin.

Posterior margin of segment 6 of peraeopod 4 with about 4 ornamental groups, each consisting of a single barb spine and a lateral seta (distalmost seta accompanied by long setae); posterior margin of segment 2 of peraeopod 7 with shallow notches, segment 4 about 40% as wide as segment 2, longest spines of segment 5 about 75% as long as dactyl, longest spines of segment 6 about 40% as long as the dactyl.

Posterior margin of epimeron 3 with about 3 shallow notches, posteroventral notch enlarged as a small tooth; rami of uropod 1 equal in length (subapical spine of inner ramus not much larger than proximal spines); outer ramus of uropod 2 shorter than inner ramus; urosomite 3 with a slight dorsal boss; rami of uropod 3 with plumose setae; each apex of telson with a stout simple seta and a plumose seta.

Clarification of the holotype. It was earlier reported (Staude, 1986) that the holotype of *Paramoera mohri* (#AHF 504) seemed erroneous, and was possibly mislabeled by Barnard (1969b) when he refigured the species. This can now be confirmed. The true holotype and paratypic specimens of *P. mohri* were found in the open collection of the Los Angeles County Museum (heir to the benthic material of the Allan Hancock Foundation). Although Barnard's (1952) original drawings are reliable, the head and urosome of the holotype are refigured here to further clarify their structure (Fig. 2). The second maxilla, which was not included in the original description, is missing from the holotype.

Barnard's juvenile Carmel specimens of *Paramoera mohri* (J. L. Barnard, 1969b, Fig. 15), as well as some specimens that I collected from Carmel Point, are *Paramoera suchaneki*, new species (p.), the only known species in which the inner rami of uropods 1 and 2 are shorter than the outer rami. True specimens of *P. mohri* of the small size (3-4 mm), collected in the present study from Carmel and from Washington, have a more prominent tooth on epimeron 3, uropod 2 with shortened outer ramus, an equiramous third uropod, and shorter telson setae.

Size range. Female to 6.5 mm, male to 5.7 mm.

Color in life. Body nearly colorless, eye dark maroon.

Distribution. Known from northern Washington (48°30'N) to central California (35°N).

Ecology. *Paramoera mohri* lives interstitially in coarse gravel and small cobble. It is primarily intertidal, migrating up and down the beach with the rise and fall of the tide, and occurs nocturnally in the nearshore plankton. Barnard (1952, 1969b, and 1975) erroneously categorized this species as an inhabitant of the rocky intertidal shore, "nestling in algae or

surfgrass." The original label of the type specimens shows that they were collected in the gravel adjacent to Hazard Canyon Reef, California.

In coastal gravel beaches *P. mohri* is sometimes found near the water's edge in concentrated densities exceeding 100,000/m², and may co-occur with lesser numbers of *P. columbiana*, *P. serrata*, *P. suchaneki*, and *Accedomoera vagor*.

The long setae of the antennae facilitate suspension feeding. *P. mohri* also feeds opportunistically on algal fragments, filamentous diatoms, and detrital deposits, and has been observed to prey on harpacticoid copepods. Ovigerous females are found throughout the year, with an average brood size of 13, but the major recruitment of juveniles occurs in the spring in Washington populations. The biology of this species has been examined in depth (Staude, 1986).

The seasonal range of water temperature at Washington collecting sites is 7-12°C (maximum recorded temperature at California sites was 17°C). This species prefers higher salinities (29-34 ppt).

Remarks. Some of the characters of the diagnosis are based largely on the Washington material (e.g., maxilla 2, oostegites, calceoli, and male gnathopods), all in close agreement with the original description and figures.

Numerous immature specimens collected subtidally from Bodega Head in 1962 are in general agreement with the diagnosis, but have slightly lighter eyes, a difference that might be an artifact of preservation. This is the only known subtidal population of *P. mohri*.

Paramoera mohri lacks a clearly distinctive identifying character. The long setae of its antennae and the plumose setae of the third uropod make it difficult to distinguish from *P. serrata* and juveniles of *P. suchaneki* and *P. columbiana*. Nevertheless, *Paramoera mohri* differs from *P. serrata* by the less developed postantennal lobe, the shallower posterior notches of the hind basal segments, the shorter spines of peraeopod 7, and the less pronounced boss of the urosome. It may be separated from immature *P. suchaneki* and *P. columbiana* by the absence of small barb spines from segment 3 of antenna 2, the shorter subapical spine of the inner ramus of uropod 1, and the absence of colored banding in life. The additional characters of the gland cone, gnathopods, peraeopod 4, telson, and body size are also useful when separating adults of these species.

***Paramoera serrata*, new species**
(Figs. 3A, 3B)

Paramoera serrata Staude, 1986: 46-62, fig. 1.6, fig. 1.7 (in part).

"*Paramoera serrata* Staude (in press)" of Staude, 1987: 376 and 378.

Material examined. Morse Creek, Washington (48°07.1'N, 123°20.7'W), NOAA Station MC+622, 27 July 1976, collected by CFN and AR from high intertidal beach (sandy gravel over buried cobble) east of stream mouth.

Holotype: female, USNM-231313; allotype, male, USNM-231314; 60 paratypes, USNM-231315; 54 paratypes, NMC-IZ1986-055.

Additional material.

WASHINGTON: Morse Creek (48°07.1'N, 123°20.7'W), NOAA Station MC+616, 17 May 1976, collected by CFN and AR from high intertidal beach (sandy gravel over buried cobble) east of stream mouth (11 specimens); Dungeness Spit (48°08.8'N, 123°11.2'W), NOAA sample number OK76302/1#5, from guts of juvenile salmon (*O. kisutch*) in beach seine collection of CS and BM (48 and 61 specimens); Dungeness Spit, NOAA Stations DS+0 and DS+3, spring 1977-winter 1978, collected by CFN and AR from low intertidal sandy-gravel beach (162 specimens); Dungeness Spit, 26 October 1984, collected by CPS and SJS in night plankton tow over low intertidal sand beach (20 specimens). CALIFORNIA: Hazard Canyon Reef (35°17.2'N, 120°52.8'W), 16 June 1982, collected by CPS from mid-intertidal fine gravel beach immediately south of reef (2 specimens); Montana de Oro Beach (35°15.4'N, 120°53.5'W), 16 June 1982, collected by CPS from mid-intertidal coarse sand beach immediately south of stack rock (5 specimens); Ebey's Landing, Whidbey Island (48°11.5'N, 122°42.5'W), 26 October 1984, collected by CPS and SJS from mid-intertidal sandy gravel beach (2 specimens).

Diagnosis. Eye moderate and dark, ovate; postantennal lobe very large, separated from the lateral lobe by a deep cleft; antenna 1 and 2 nearly equal in length; major peduncular segments of antennae with 5 or more groups of long setae along the ventral margins; gland cone with 4-6 long setae.

Inner plate of maxilla 1 with 5-7 plumose setae; inner plate of maxilla 2 with 4 plumose setae in the diagonal row

Segment 6 of gnathopod 1 with 5-6 posterior groups of comb setae; segment 6 of gnathopod 2 with 6-10 posterior groups of comb setae; in female segment 5 of gnathopod 2 about 70% as long as segment 6; in male segment 5 of gnathopod 2 about 45% as long as segment 6, palm of gnathopod 2, very oblique, palm about 75% as long as the posterior margin.

Posterior margin of segment 6 of pereopod 4 with 3 ornamental groups, each consisting of a single barb spine and a curved seta on its lateral side (the distalmost spine enlarged and accompanied by additional long setae); posterior margin of segment 2 of pereopod 7 serrated, segment 4 nearly 50% as wide as segment 2, segments 5-6 with long spines (some as long as the dactyl).

Posterior margin of epimeron 3 with 2 distinct notches, the notch at the posteroventral corner bounded by a small recurved tooth; peduncle of uropod 1 with 7-10 lateral spines; urosomite 3 with a dorsal boss; inner ramus of uropod 3 with plumose setae along the entire inner margin and at the tip of the outer margin, outer ramus with plumose setae along the distal half of the inner margin; each apex of telson usually with 1 slender spine and a plumose seta (occasionally 1-2 stout barb spines at each apex).

Coxal gill of pereopod 7 small, present only in female.

Size range. Female to 6.0 mm, male to 4.6 mm.

Color in life. Body and all appendages translucent white with very faint pink banding along the sutures of pereonites, eye red.

Distribution. Known from the Washington shore of the Strait of Juan de Fuca (latitude 48°N) to central California (35°N), with a distinctive southern subspecies found in Baja California (32°N).

Ecology. *Paramoera serrata* is a shallow burrower in coarse sand and gravel sediments of wave exposed beaches. The widened posterior pereopods with enlarged spines may be an adaption to this burrowing habit (e.g., similar to some species of the Haustoriidae). The well-developed, regularly spaced setae of the antennae and gnathopods are probably used in suspension feeding. The nocturnal presence of this species in the plankton is similar to the behavior of *P. mohri*. Brood size is about 12 ova. Recorded water temperatures at the collecting sites range from 6.3°C (winter) to 11.2°C (summer), with a mean salinity of 29.4 ppt (Nyblade, 1979).

Remarks. *Paramoera serrata* exhibits several derived characters, and seems to occupy a niche that is somewhat removed (although not exclusive) from its congeners. The expanded postantennal lobe of the head, the subequal length of the antennae, the extremely setose maxillipedal palp, the enlarged distal spine of pereopods 3 and 4, the long spines of pereopods 5-7, and the boss of urosomite 3 are unique. The serration of segment 2 of pereopods 5-7, and the sculpture of epimeron 3 are distinctive characters similar to those of the new subgenus *Humilomoera*. The exceptionally setose antennae and gland cone suggest an affinity to *Paramoera suchaneki*, new species (See "Remarks" under *P. mohri* for identification of juveniles).

Etymology. The species name refers to the serrated posterior margins of the basal segments of pereopods 5-7.

Paramoera serrata escofetae, new subspecies
(Fig. 4)

Paramoera serrata Staude, 1986 (in part): 49, 59-62.

Material examined.

BAJA CALIFORNIA: Grenada Cove, Ensenada, Mexico (31°53'N, 116°41'W), 1 March 1980, collected by AE from low intertidal cobble beach (32 specimens).

Holotype: female (LACM #94-41.1), allotype, male (LACM #94-41.2); 30 paratypes (LACM #94-41.3 and CPS).

Diagnosis. This subspecies is closely similar to the northern form of *P. serrata* in having subequal antennae with long filtering setae, a deep cleft of the inferior antennal sinus,

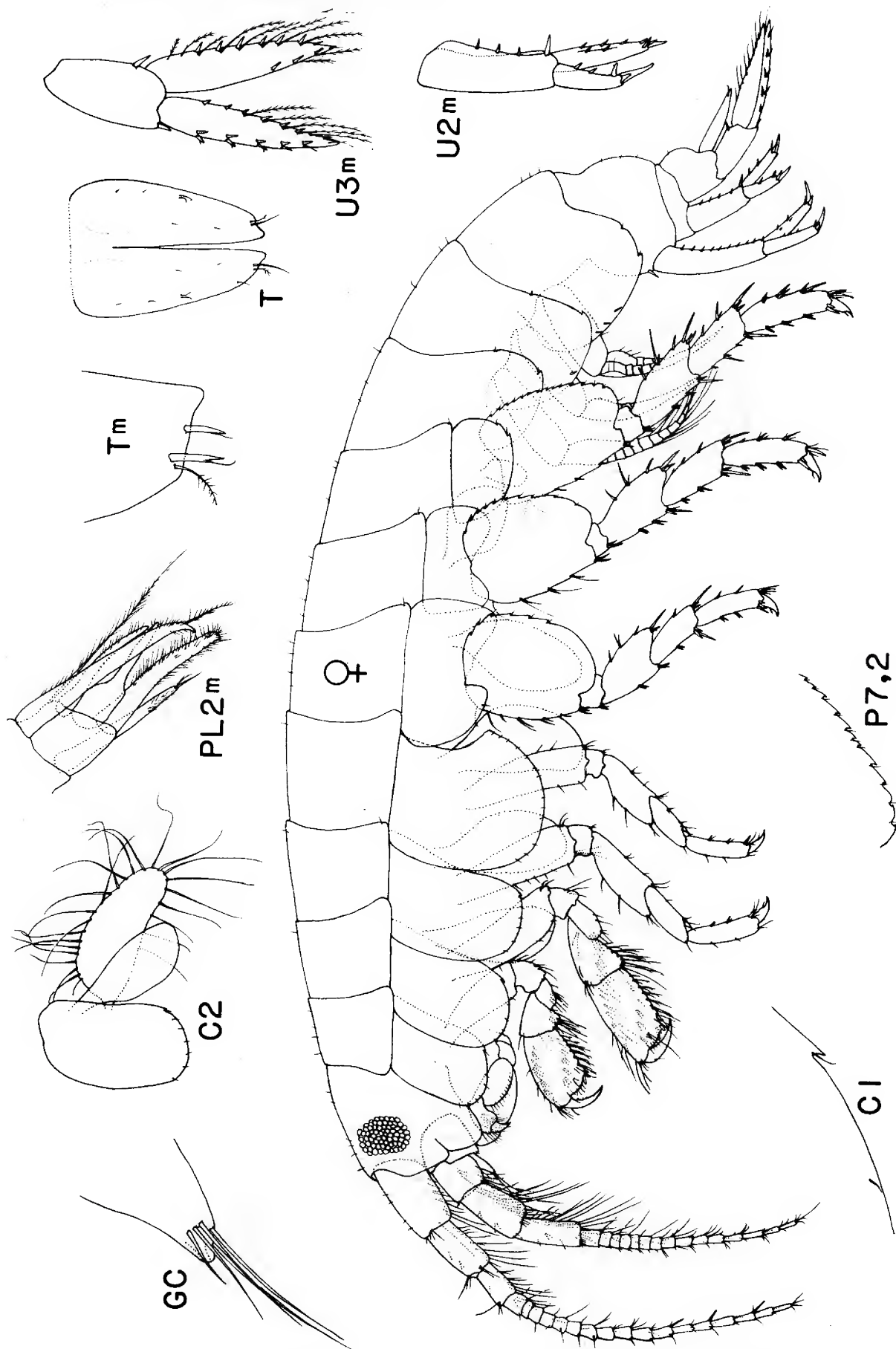


FIG. 3A. *Paramoera serrata*, new species. Holotype female (4.3 mm). m = allotype male (4.0 mm). Morse creek, WA.

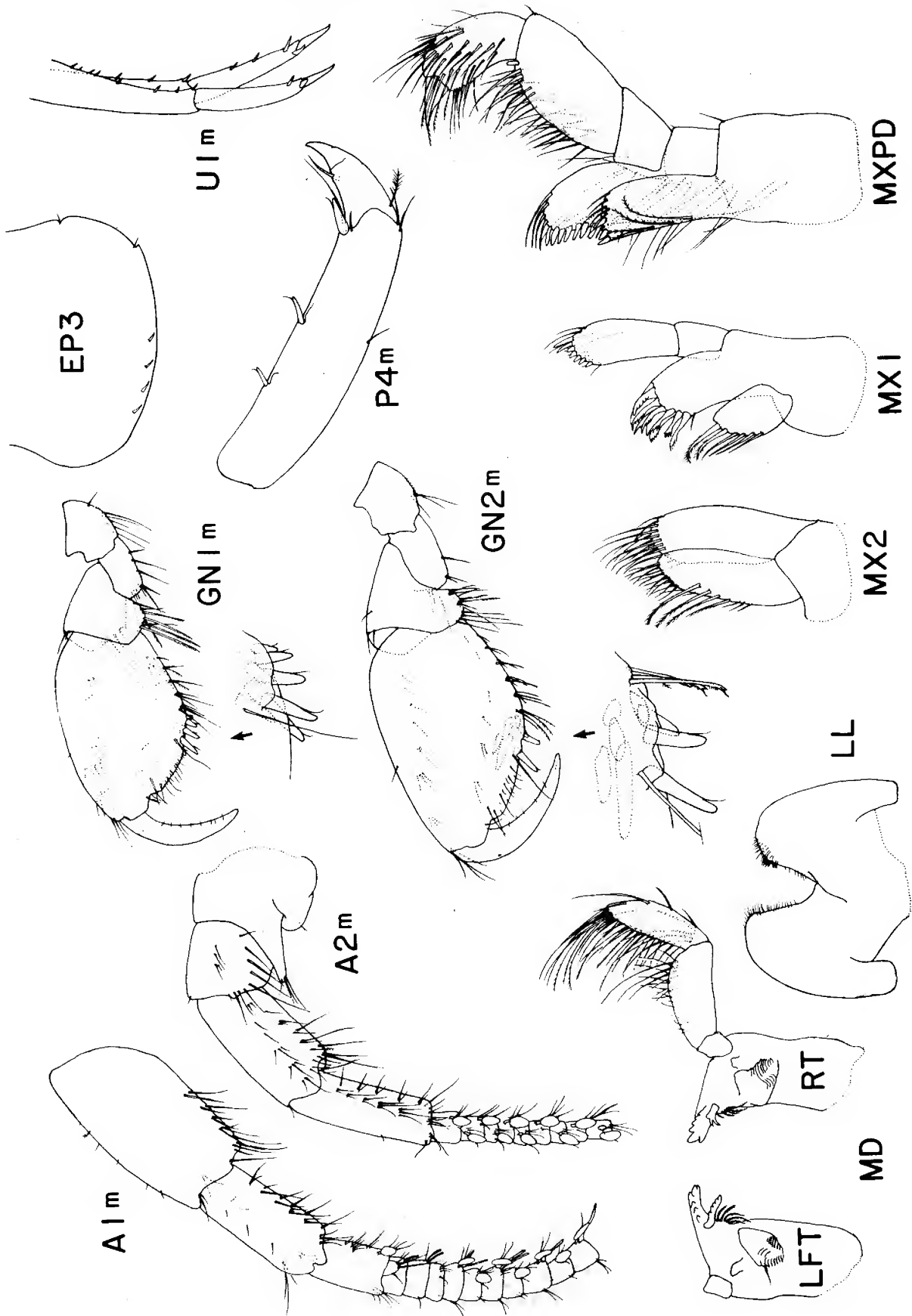


FIG. 3B. *Paramoera serrata*, new species. Holotype female (4.3 mm). m = allotype male (4.0 mm). Morse creek, WA.

similar mouth parts, a very setose gland cone and gnathopods, similar ornamentation of the epimera, and a single slender spine on each apex of the telson. They are distinct from northern *P. serrata* by the more spinose segment 6 of pereopod 4, the less serrated posterior margins of segment 2 of pereopods 5-7, the shorter distal spines of segments 4-5 of pereopod 7, and the less pronounced boss of urosomite 1. The eye is unpigmented (perhaps an artifact of preservation).

Size range. Female to 7.0 mm, male to 6.0 mm

Color in life. Unknown

Distribution. Known only from the type locality, Baja California (latitude 32°N).

Ecology. The type locality is a beach of clean cobbles and sand that is seasonally resorted by wave action. This habitat is unusual for the northern *P. serrata*, which prefers coarse sand and gravel. The Ensenada population may instead be concentrated in a shallow subtidal sand berm, which is adjacent to these intertidal cobbles (pers. obs. of 12 June 1982). Females collected in March were ovigerous, with about 12 eggs.

Remarks. Specimens collected at Ensenada, Mexico, are recognized here as a southern subspecies of *P. serrata*, but possibly constitute a separate species. Its status may be resolved by future collections and studies of its behavioral ecology, in contrast to the northern form.

Etymology. This subspecies is named in honor of Ms. Anamaria Escofet, professor of biology at Centro de Invest. Cientificas, in Ensenada, Baja California, Mexico, who collected these specimens. Professor Escofet has also contributed to our knowledge of the amphipod fauna of Argentina.

***Paramoera suchaneki*, new species**
(Figs. 5A, 5B)

Paramoera mohri J. L. Barnard, 1969b: 110-111, fig. 15.-- Barnard, 1975: 348 and 362 (in part), pl. 73, fig. 38.

Paramoera cf. *mohri* Suchanek, 1979: 136, Appendix VI.

Paramoera suchaneki Staude, 1986: 63-82, figs. 1.8 and 1.9.

"*Paramoera suchaneki* Staude (in press)" of. Staude, 1987: 376 and 378.

Material examined.

Tatoosh Island, Washington (48°24'N, 124°44'W), Suchanek Station T/5L, May and July 1976, collected by THS in mussel bed (*M. californianus*), low intertidal, wave-exposed, rocky beach.

Holotype: female, USNM-231316; allotype, male, USNM-231317; 8 paratypes, USNM-231318; 2 paratypes, NMC-IZ1986-055.

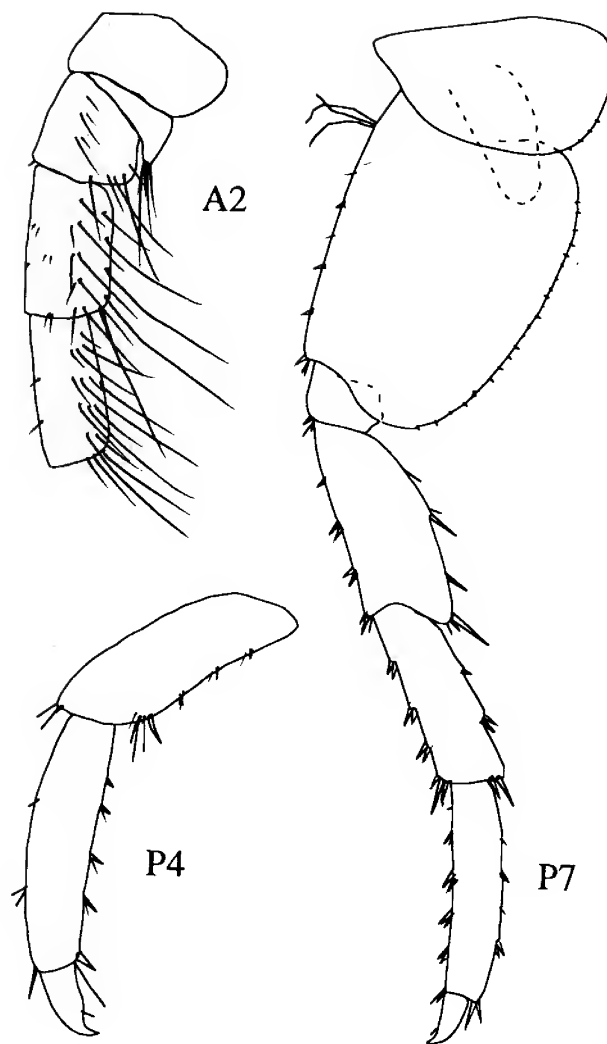


FIG. 4. *Paramoera serrata escofetae* n. s-sp. female holotype (6.5 mm), Ensenada, Mexico. (A2 in medial view).

Additional material.

ALASKA: Hogan Island, S.E. Alaska (57°43'N, 136°15'30"W), NMC Station S5B10, 28 July 1980, collected by ELB under open stones, mid-intertidal (1 female); Dry Pass, Hill Island, Chichagof Island (57°47'N, 136°18'W), NMC Station S7B6, 29 July 1980, collected by ELB under bare stones, mid- to high intertidal (1 immature female); Trap Point, Slocum Arm, Chichagof Island (57°33.5'N, 136°01'W), NMC Station S3B2, July 1980, collected by ELB beneath kelp zone, low to mid-intertidal (1 immature female); Column Point, Lisianski Strait (58°06.5'N, 136°27'W), NMC Station S11B4-5, July 1980, collected by ELB intertidally under open boulders (1 ovigerous female, 1 male).

BRITISH COLUMBIA: Nesto Point, Graham Island (53°27'N, 132°48'W), NMC Station W4a, 11 August 1957, collected by ELB among shell fragments and boulders, low intertidal (3 specimens).

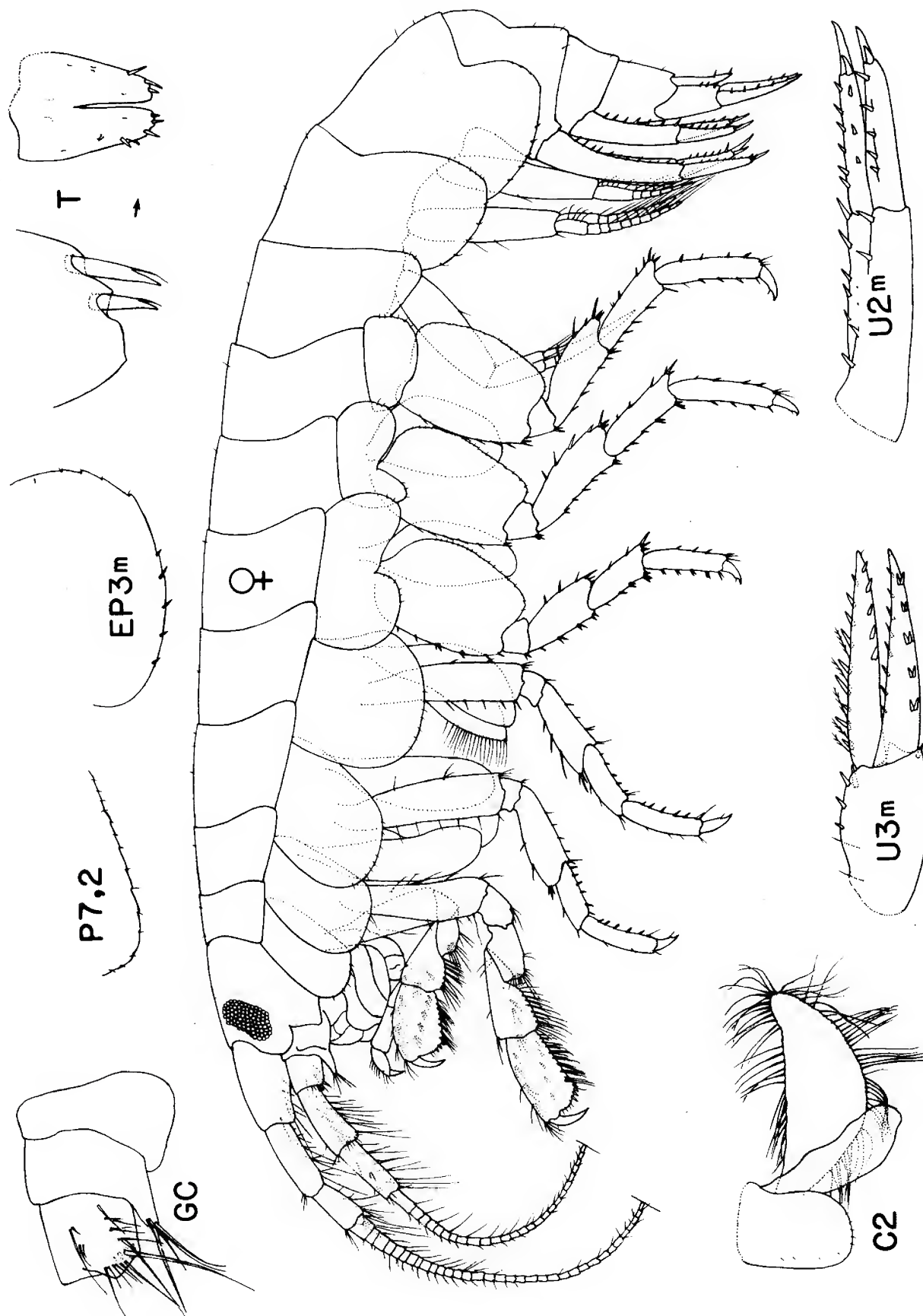


FIG. 5A. *Paramoera suchanekei*, n. sp. holotype female (12.0 mm); m = allotype male (8.0 mm). Tatoosh I., WA.

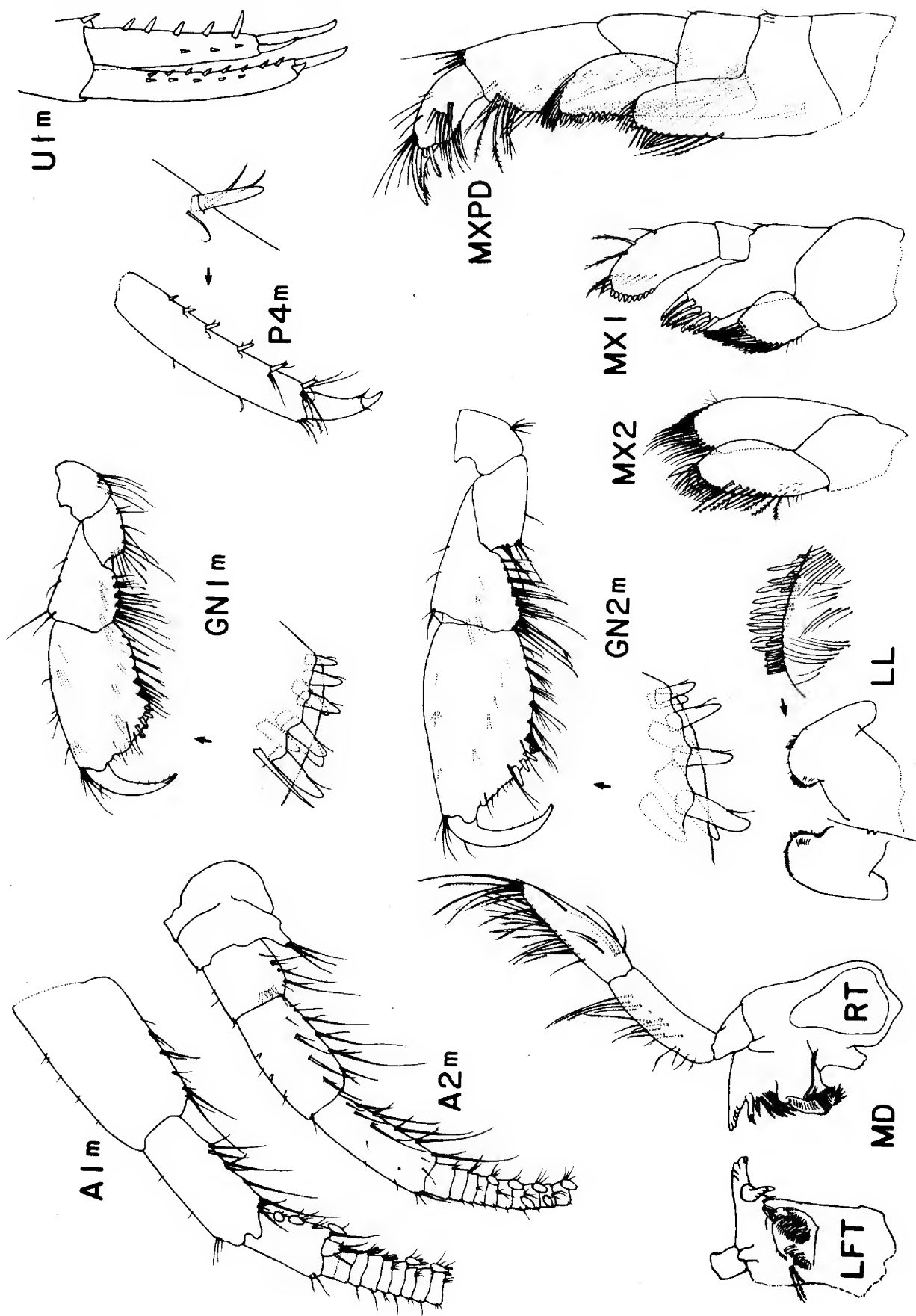


FIG. 5B. *Paramoera suchaneki*, n. sp. holotype female (12.0 mm); m = allotype male (8.0 mm). Tatoosh I., WA.

WASHINGTON: Tatoosh Island (48°24'N, 124°44'W), Suchanek Stations T/2, T/4, and T/5, July 1974, April and September 1975, May and July 1976, replicate samples collected by THS in mussel bed (*M. californianus*), low to mid-intertidal, wave-exposed, rocky beach (>200 specimens); Shi-Shi Beach (48°17'N, 124°41'W), Suchanek Station S/1, July 1974, April and September 1975, May and July 1976, replicate samples collected by THS in mussel bed (*M. californianus*), mid-intertidal, rocky bench (>100 specimens); Goose Island (48°27.5'N, 122°57.3'W), 16 April 1983, collected by CPS under cobbles on gravel and sand, mid- to high intertidal (25 specimens); Deadman Bay, San Juan Island (48°30.7'N, 123°08.7'W), Staude Station C, 15 July 1983 and monthly samples January-December 1984, collected by CPS under cobbles and among boulders on sand and gravel, mid-intertidal (>100 specimens).

CALIFORNIA: Carmel Point (36°32'N, 121°56'W), Barnard Station 48-X-1, 30 December 1963, collected by JLB intertidally from unknown substratum (4 of 7 specimens; AHF collection); Carmel Point (36°32'N, 121°56'W), Staude Site 4, 18 June 1982, collected by CPS from intertidal pockets of gravel among rocks (4 specimens).

Diagnosis. Eye large and dark, slightly reniform; inferior antennal sinus with a small cleft; antenna 1 about 10% longer than antenna 2; peduncles of antennae with 4-6 groups of long setae along the ventral margins of each segment; gland cone with about 5 long setae; inner plate of maxilla 1 with 9-11 plumose setae along the inner margin; inner plate of maxilla 2 with 6-9 plumose setae in the diagonal row; segment 6 of gnathopod 1 with 6-8 groups of comb setae along its posterior margin; segment 6 of gnathopod 2 with 7-10 groups of comb setae along its posterior margin; in male segment 5 of gnathopod 2 about 80% as long as segment 6, palm of gnathopod 2 oblique, palm about 60% as long as posterior margin of segment 6; in female segment 5 of gnathopod 2 greater than or equal in length to segment 6, palm of gnathopod 2 nearly transverse, palm about 30% as long as the posterior margin of segment 6; posterior margin of segment 6 of peraeopod 4 with a row of about 6 ornamental groups, each consisting of a single barb spine with a small curved seta on either side; posterior margin of segment 2 of peraeopod 7 minutely serrated, segment 4 about 40% as wide as segment 2, largest spines of segments 5 and 6 less than 33% as long as the dactyl; posterior margin of epimeron 3 minutely serrated, with a small seta emerging from each of 5 or 6 slight notches; posteroventral corner of epimeron 3 not strongly developed; uropod 3 with plumose setae proximally along the inner margin of the inner ramus and often with a few plumose setae proximally along the inner margin of the outer ramus; each lobe of the telson with 2-3 short apical spines and a longer proximal spine; gills especially long, but lacking a gill on peraeopod 7 in both sexes.

Size range. Female to 13 mm; male to 10 mm.

Color in life. Antennae with red-brown tint; eye nearly

black; peraeonites with dorsal pigment patches which form a symmetrical mottled pattern about the sagittal midline, these patches either brown or olive. Pleon of some Alaskan specimens with a pink tint. Juveniles with purple banding at sutures of peraeonites.

Distribution. Known from Southeast Alaska (latitude 58°N) to northern California (latitude 36°30'N).

Ecology. *Paramoera suchaneki* is a nestler at the base of boulders and rocks on gravel/sand in the mid intertidal zone with moderate to strong wave exposure. It is occasionally abundant interstitially among the byssal threads, shells, and associated detritus of dense mussel beds (*Mytilus californianus*). Its setose antennae and gnathopods are presumed to assist it in the collection of suspended chain-forming diatoms and algal fragments as well as settled detritus. Washington populations occur at salinities of 28-32 ppt, and temperatures of 8-15°C.

Remarks. With maturity, the eye becomes more reniform, antennae and gnathopods become more setose, and peraeopods become more spinose. Hence, juveniles are easily confused with other species, but may be distinguished by the shorter inner ramus of uropods 1 and 2.

This species was mistaken for *Paramoera mohri* by J. L. Barnard (1969b; his Fig. 15), and is lumped with *P. mohri* in his later work (J. L. Barnard, 1975).

There is a surprising degree of similarity between *Paramoera suchaneki* and *P. australis* (Bate, 1862) of the southern hemisphere. Comparison to a redescription (M. H. Thurston, unpub.) of Bate's type specimens indicates that the head, antennae, gland cone, mouthparts, gnathopods, peraeopods, epimera, uropods, and telson are in fairly close agreement, except as follows: *P. australis* with setae of antennae shorter and less abundant, maxilla 2 with diagonal setal row extending 50% across the face of the inner plate, dactyls of gnathopods with minutely serrate inner margin, segment 6 of peraeopod 4 apparently with 2-3 spines in each spine group of the posterior margin (although segment 6 of peraeopod 3 seems to have only single spines), uropod 1 with 27 spines along the lateral margin of the peduncle and 14 spines along the lateral margin of the outer ramus, uropod 2 outer ramus slightly shorter than the inner ramus, uropod 3 apparently without plumose setae, each lobe of telson with an additional proximal spine near the lateral margin (about 60% back from the apex).

Similarities are also recognized between *P. suchaneki* and *P. koreana* Stephensen 1944. The antennae, gnathopods, peraeopods, and uropod 3 are in close agreement in these species. However, *P. koreana* is distinguished by the single seta on the gland cone, the reduced setosity of the maxillae, the distinct tooth at the posteroventral corner of epimeron 3, the greater spinosity of uropod 1 (while lacking the enlarged distal spine of the peduncle), the single seta on each lobe of the telson, and the smaller size at maturity (5 mm).

Paramoera brevirostrata (Bulytscheva, 1952), originally

recognized as *Pontogeneia* and more recently placed in *Accedomoera* (Thurston, 1972), also exhibits similarity to *P. suchaneki* in the eye, antennae, gland cone, and gnathopods. Comparison to Bulyscheva's original illustrations (which are lacking in detail) would suggest that *P. brevirostrata* can be distinguished by the apparent lack of a cleft in the inferior antennal sinus, the fewer setae on the inner plates of maxilla 2 and maxilliped, the more setose margins of coxae 1 and 2, the lack of plumose setae on uropod 3, and the shape and ornamentation of the telson (each acutely tapered lobe with a single seta). It should be noted that in 1972 Barnard suggested that *P. brevirostrata* was a "probable synonym" of *P. japonica* (Tattersall, 1922). More recently, however, Barnard & Karaman (1982) have transferred *japonica* to the genus *Sternomoera*. The setose nature of the telson, the sternal gills, and the freshwater habitus of *S. japonica* are quite distinctive, and warrant continued separation of these species.

Etymology. Named in honor of Dr. Thomas H. Suchanek, who originally discovered this species in his studies of the *Mytilus californianus* community. This and other research performed on Tatoosh Island under the supervision of Dr. Robert T. Paine have greatly increased our knowledge of the ecology of rocky shores.

Paramoera columbiana Bousfield

Paramoera columbiana Bousfield, 1958: 62-64, figs. 1, 2.-- Bousfield & Hubbard, 1968: 2-3.-- Staude, 1986: 83-88, fig. 1.10.--Staude, 1987: 376 and 378.

Material examined.

ALASKA: Amchitka Island (51°28'N, 179°07'E), O'Clair Station IA-2, plot 9, 23 October 1972, collected by CEO on uplifted bedrock reef (1 specimen; NMC 1976-30); St. Paul Island, Pribilof Islands (57°10'N, 170°30'W), 30 November 1979, collected by CEO from high intertidal lagoon (1 specimen); Olsen Bay, Prince William Sound (60°45.5'N, 146°11'W), NMC Station SB2, August 1965, collected by JDH at the mouth of Olsen Creek (1 specimen); Steamer Bay, Etolin Island (56°08'N, 132°40'W), summer 1981, collected by MLM from cobble sediment in the tidal reach of Porcupine Creek (10 specimens); Port McArthur Bay, Kuiu Island (56°05'N, 134°10'W), NMC Station A15, collected by ELB (1 specimen); Pt. Marsh, Prince of Wales Island (54°43'N, 132°17'W), NMC Station A5, collected by ELB (3 specimens).

BRITISH COLUMBIA: Hay's Creek, Prince Rupert (54°18'N, 130°20'W), NMC Station P3, 3 July 1957, collected by ELB from mouth of creek (2 specimens; ELB slide mount); Kitimat (54°02'N, 128°45'W), 7 October 1981, Station DS441, collected by SC from intertidal beach (4 specimens); Queen Charlotte City (53°16'N, 132°04'W), NMC Station E8, 17 August 1957, collected by ELB from

stones and moss in small stream (>50 specimens); Stiu Point, Graham Island (53°14'N, 132°36'W), NMC Station W6, 29 July 1957, collected by ELB from bedrock pools at stream mouth (11 specimens); Gray Bay, Moresby Island (53°08'N, 131°43'W), NMC Station E21, 12 July 1957, collected by ELB from high intertidal, freshwater pools on a rock and boulder shore (holotype, allotype, and 24 paratypes; NMC 2277); Cape Fanny, Moresby Island (52°07'N, 131°09'W), NMC Station W6, collected by ELB from stream mouth (1 specimen); Dutchman Head, Knight Inlet (51°05'N, 125°35'W), NMC Station N14, 25 June 1959, collected by ELB from intertidal fine silt and fucoids on bedrock (3 of 14 specimens); Simms Creek, Vancouver Island (49°48'N, 125°11'W), NMC Station V21, 28 July 1959, collected by ELB from coarse sand and stones with woody detritus in in brackish water (5 specimens); Porteau Cove, Howe Sound (49°33'N, 123°14.2'W), collected by CL from unknown substratum (14 of 39 specimens); Cowichan River estuary, Vancouver Island (48°46'N, 123°36'W), 9 February 1978, collected by ELB from *Fucus* and leaf litter (8 of 17 specimens); Mount Douglas Beach, Victoria (48°30'N, 123°20.3'W), 20 April 1983, collected by PS from high intertidal (2 specimens); Muir Creek, Vancouver Island (48°22.8'N, 123°52'W), 1 May 1983, collected by PS at mouth of creek (18 specimens).

WASHINGTON: Deadman Bay, San Juan Island (48°30.7'N, 123°08.7'W), Staude Station B, 1 June 1983, collected by CPS on low intertidal gravel beach (2 specimens); Morse Creek (48°07.1'N, 123°20.7'W), NOAA Station MC+004, 17 May 1976, collected by CFN and AR from low intertidal beach (sandy gravel and cobble) east of stream mouth (2 specimens); Carkeek Beach, Seattle (47°42.8'N, 122°22.7'W), METRO Station C7+613, collected by JWA and CPS from mid-intertidal mixed sediment beach near small stream (2 specimens).

Diagnosis. Eye large and dark, reniform; postantennal sinus with a cleft; antenna 1 about 10% longer than antenna 2; segment 1 of antenna 1 with 2-3 short barb spines at the distoventral corner; major peduncular segments with about 3 groups of moderate length setae along the ventral margins (reduced in male), gland cone of female with 1-2 barb spines and 1-2 setae, male with 2-3 barb spines (no setae).

Inner plate of maxilla 1 with 5-6 plumose setae; inner plate of maxilla 2 with 4-5 plumose setae in the diagonal row.

Segment 6 of gnathopod 1 with 3-4 posterior groups of comb setae; segment 6 of gnathopod 2 with 5-6 posterior groups of comb setae and with sparse mesial setae; gnathopod 2 of female with segment 5 about 20% longer than segment 6; gnathopod 2 of male with segment 5 about as long as segment 6, palm very oblique and poorly defined, about as long as the posterior margin.

Posterior margin of segment 6 of pereopod 4 with about 5 ornamental groups, each consisting of 2-3 barb spines; posterior margin of pereopod 7 with shallow notches, segment 4 about 40% as wide as segment 2, spines of segments 5 and

6 not longer than 55% of the dactyl.

Posterior margin of epimeron 3 with 2-6 shallow setose notches, posteroventral corner with a minute tooth (without seta); uropod 2 with outer ramus only slightly shorter than the inner ramus; uropod 3 with plumose setae; each apex of telson with 1 barb spine, 1 long stout seta, and a small plumose seta.

Coxal gills small; coxa 7 with gill (both sexes).

Size range. Both sexes to about 9 mm (11 mm in northern populations).

Color in life. Body translucent with purple banding; eye dark.

Distribution. West to Amchitka Island (179°E), and from the Pribilof Islands (57°N) to central Puget Sound (47°40'N).

Ecology. *Paramoera columbiana* has been widely collected in a variety of habitats (e.g., spray pools, rock benches, and tidal reach of streams). It is apparently euryhaline, but is frequently found in areas of reduced salinity near stream mouths. The presence of both spines and long setae on the antennae suggests an omnivorous diet. Oviparous females have been found from May to July. Fecundity is high in this species; up to 41 eggs per brood. The absence of modified pleopods in the male further suggests that the reproductive biology of *P. columbiana* is different from that of other local species of the *Paramoera* group.

Remarks. Juveniles are particularly difficult to distinguish from *P. mohri* and *P. suchaneki* because the spinosity of the gland cone, pereopod 4, and the telson increases with maturity. Immature specimens of *P. columbiana* can be recognized by the presence of barb spines distally on the ventral margin of segment 1 of antenna 1 and the dorsal margin of segment 3 of antenna 2, and by the enlarged subapical spines on the inner rami of uropods 1 and 2.

The number of setose notches along the posterior margin of epimeron 3 is variable (holotype with 6, and male paratype with 4), while specimens from Steamer Bay, Alaska (5 mm immature female), and Seattle, Washington (8 mm brooding female) have as few as 2. In nearly all cases the posteroventral tooth of epimeron 3 is very small and asetose.

This is the only local species of *Paramoera* (*sensu lato*) known to exhibit sexual dimorphism in the ornamentation of the gland cone. The palm of gnathopod 2 is also sexually modified. It is the only species of this group to lack the gonopodous condition of the second pleopod in the male.

An 11 mm immature female (with early stage oostegites) from the Pribilof Islands was examined. Its characters are in general agreement with the diagnosis (some exceptions being the more setose gnathopods and an additional barb spine on one apex of the telson), but its large size suggests a northern race of *P. columbiana* with a modified life history pattern.

Paramoera bousfieldi, new species
(Figs. 6A, 6B)

"*Paramoera* undescribed species" Armstrong et al., 1976.
"undescribed species near *Paramoera mohri*" Staude et al., 1977.

Paramoera bousfieldi Staude, 1986: 89-103.

"*Paramoera bousfieldi* Staude (in press)" of Staude, 1987: 376-378.

Material examined.

Indian Beach, San Juan Island, Washington (48°27.4'N, 122°57.7'W), 18 May 1984, collected by CPS under cobbles and in shallow sand deposits over a hard clay bench, mid-high intertidal.

Holotype: female, USNM-231319; allotype, male, USNM-231320; 18 paratypes, USNM-231321; paratypes, NMC-IZ1986-055.

Additional material.

ALASKA: Rakof Island, Dry Pass (56°44.5'N, 135°18.5'W), NMC Station S20B4, 3 August, 1980, collected by ELB under stones in eel grass, low intertidal, stream mouth (1 specimen).

BRITISH COLUMBIA: Nesto Point, Graham Island (53°27'N, 132°48'W), NMC Station W4a, 12 August 1977, collected by ELB from low intertidal shell fragments and boulders over bedrock (2 specimens); Horn Rock, Tasu Sound (52°46'N, 132°03'W), NMC Station W16, 10 August 1957, collected by ELB in high water pools (2 specimens); McNab Creek, Howe Sound (49°33.8'N, 123°22.8'W), 21 March 1973, collected by CL near stream mouth (55 specimens); Sarita River Estuary, Barkley Sound (48°53.2'N, 125°00.5'W), NMC Station B14, 2 July 1976, collected by ELB under stones at stream mouth (2 specimens); Victoria Breakwater (48°24.8'N, 123°23'W), 1976, collected by RJL (1 specimen).

WASHINGTON: Lincoln Park Beach, Seattle (47°31.7'N, 122°23.8'W), July 1974, METRO transect 15, collected by JWA and CPS from high intertidal seepage area in shallow mixed sediment over a clay bench (21 specimens); Tongue Point, Strait of Juan de Fuca (48°10'N, 123°40.2'W), NOAA Station TP+3(04), 1 May 1976, collected by CFN and AR from mid intertidal rocky beach (1 specimen); Tatoosh Island (48°24'N, 124°44'W), Suchanek Station T4H, July 1976, collected by THS in high intertidal mussel community (1 specimen); Long Beach (46°19'N, 124°04'W), NMC Station W45, 3 July 1966, collected by ELB from intertidal surf-pounded sand over bedrock (1 specimen).

OREGON: Tillamook Bay (45°30.5'N, 123°56.5'W), NMC Station W65, 17 August 1966, collected by ELB from intertidal coarse sand over clay and embedded stones, brackish (1 specimen).

Diagnosis. Eye large and dark, ovate; inferior antennal sinus deep, with a shallow cleft; antenna 1 about 25% longer than antenna 2; peduncles of antenna 2 with 2-3 groups of

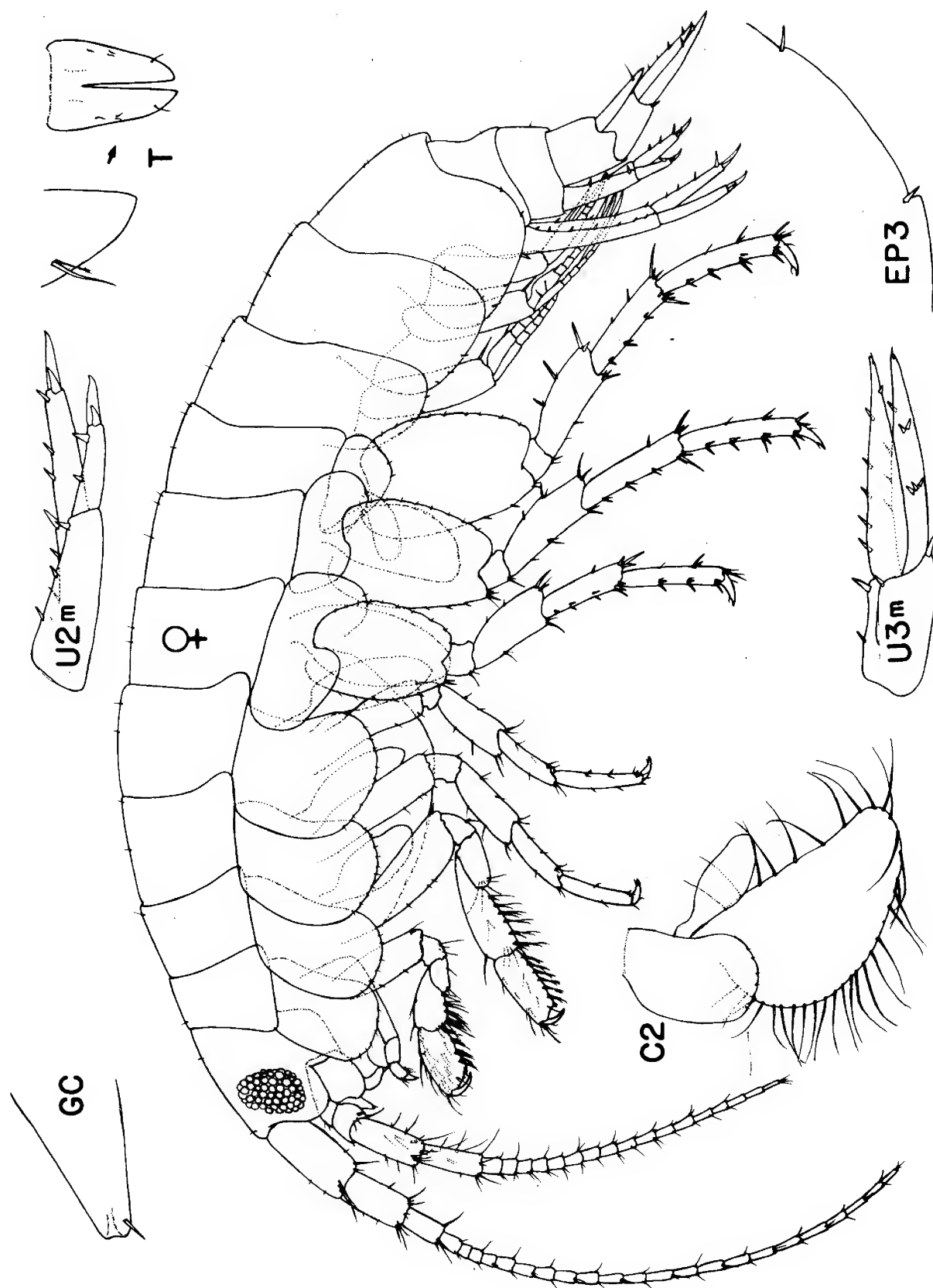


FIG. 6A. *Paramoera bousfieldi*, n. sp. holotype female (4.3 mm); allotype male (3.0 mm). San Juan Island, Washington.

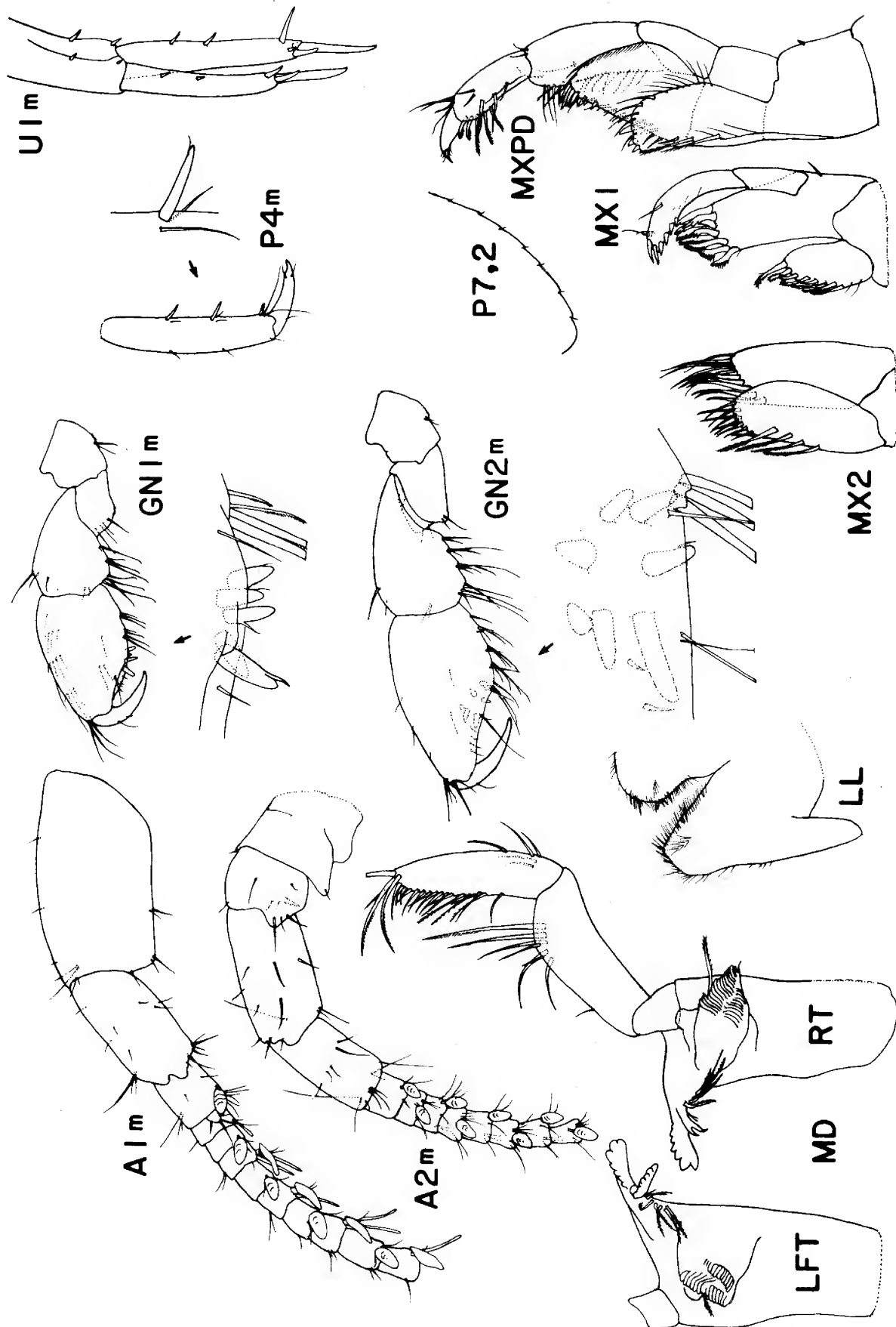


FIG. 6A. *Paramoera bousfieldi*, n. sp. holotype female (4.3 mm); allotype male (3.0 mm). San Juan Island, Washington.

medium-length setae along the ventral margins of each segment; gland cone with a single short seta.

Inner plate of maxilla 1 with 6-7 plumose setae; inner plate of maxilla 2 with 4 plumose setae in the diagonal row.

Segment 6 of gnathopod 1 with 3 groups of comb setae along the posterior margin; segment 6 of gnathopod 2 with 4-6 groups of comb setae along the posterior margin; in male segment 5 of gnathopod 2 about 85% as long as segment 6, palm of gnathopod 2 very oblique, palm nearly equal in length to the posterior margin; in female segment 5 of gnathopod 2 about 135% as long as segment 6, palm of gnathopod 2 about 20% as long as the posterior margin; posterior margin of segment 6 of pereopod 4 with a row of 3 ornamental groups, each consisting of a slender barb spine and 1-2 setae; posterior margin of pereopod 7 minutely serrated, segment 4 about 40% as wide as segment 2, largest spines of segments 5 and 6 about 75% as long as the dactyl.

Posterior margin of epimeron 3 with a single notch and seta proximal to a slightly enlarged tooth-like notch and seta at the posteroventral corner; uropod 3 lacking plumose setae; each lobe of telson rather acutely pointed, lacking apical notches or spines, but with a long slender spine subapically near the lateral margin; size to about 4.5 mm.

Size range. Male to 4 mm; female to 4.5 mm.

Color in life. Body translucent white, with light purple banding at articulations of pereonites and pleonite 1; similar purple blushing on antennae and posterior margins of coxae; eye reddish.

Distribution. Known from southeast Alaska (56°N) to northern Oregon (45°30'N).

Ecology. Commonly occurring under rocks or in shallow sediment deposits at stream mouths or freshwater seeps where temperature and salinity fluctuate widely over the course of the tidal cycle. Its exact position on the beach is determined more by seepage than tide level. Gnathopods have a full complement of comb setae, but setosity of antennae is reduced, suggesting that surface deposit feeding is of greater importance than suspension feeding in this species. Brood size ranges from 13-19 eggs.

Remarks. *Paramoera bousfieldi* is set apart from the other members of the grade "*Paramoera*" by a number of apomorphic characters. The cleft of the inferior antennal sinus is minute, the antennal setae are reduced, the setosity of the maxillae is intermediate, the brood plates are of the broad form, and the third uropod lacks plumose setae. The palm of gnathopod 2 in the male is very oblique, as in *P. columbiana*. The setosity of the maxillae, the elongate carpus of gnathopod 2 in the female, and the slender distal segments of the posterior pereopods bear resemblance to characters of the subgenus *Moanamoera*.

Etymology. Named in honor of Dr. E.L. Bousfield, who

originally discovered this species in 1957 (unpublished). Through his many years of field collection and museum research, Dr. Bousfield has become the foremost authority on gammaridean amphipods of the eastern North Pacific region.

Paramoera (Moanamoera), new subgenus

Type species. *Paramoera (Moanamoera) rua* J. L. Barnard, 1977.

Diagnosis. Rostrum unproduced; lateral cephalic lobe mammiliform; inferior antennal sinus shallow and without a cleft. Eye reduced or absent, oval, unpigmented. Antennae of moderate length, antenna 1 not much longer than antenna 2; peduncular segments of antenna 1 progressively shorter, segment 1 shorter than head; accessory flagellum 1-segmented, scale-like; ventromedial setae of peduncles short; gland cone with 2-3 moderate setae; calceoli present only in male.

Upper lip entire and subrounded; epistome unproduced. Molar triturative, oval; palp segment 2 longer than 3; lower lip without distinct inner lobes. Maxilla 1: inner plate with 7-10 plumose setae, outer plate with 9-10 pectinate spines; palp long, segment 1 short. Maxilla 2: inner plate not broader nor longer than outer plate, inner plate with a submarginal row of 4-5 plumose setae. Maxilliped: inner plate about as long as outer plate, outer plate with about 8-10 medial spine teeth; palp of 4 segments, segment 1 with a small distolateral extension (but its lateral margin distinctly shorter than that of segment 2), segment 3 with a slight distal lobe, segment 4 shorter than segment 3, segment 4 not spinose (but with small distal setae) along the inferior margin, ungiform, with nail.

Coxae 1-3 distinctive, elongate and with several moderate setae on the posterior half of their medial faces, ventral margins sparsely set with short setae, the posteroventral seta emerging from a small notch; coxa 4 with posterior lobe, excavate; anterior lobe of coxa 6 not produced, ventral margin of coxa 6 without spines. Gnathopods slender, not eusirid, with subchelate oblique palm; segment 5 of gnathopod 2 longer than segment 6 in female; gnathopod 2 of male not enlarged, palm with less than 4 barb spines in the outer row.

Dactyls of pereopods 3-7 non-castellate, with 2 small setae near the uncinus; segment 2 of pereopods 3 and 4 not anteriorly lobate; pereopod 5 nearly as long as pereopod 7; segment 2 of pereopods 5-7 very broad, subcircular, posteroventrally lobate, that of pereopod 7 with a posterodorsal lobe; segment 5 of pereopods 5-7 shorter than segment 6.

Pleopods ordinary; pleopod 2 of male gonopodous. Posteroventral corner of epimeron 2 acutely produced; epimeron 3 with 1-3 shallow posterior notches. Peduncles of uropods 1 and 2 not dorsally broadened; rami of uropod 1 subequal; outer ramus of uropod 2 shorter than inner ramus. Uropod 3 extending beyond uropod 1; peduncle without a large process; rami equal in length, narrow, lanceolate, with plumose setae. Lobes of telson fused less than a quarter of its length, apical margins tapered or notched, with 2 or more

setae.

Coxal gills present on pereopods 2-6 in both sexes; gills moderate but shorter than anterior coxae. Sternal gills absent. Female with large oostegites on pereopods 2-4 and a smaller strap-like oostegite on pereopod 5; oostegite of pereopod 2 narrow, not wider than this coxa.

Relationships. The subgenus *Moanamoera* is like the grade "*Paramoera*" (defined above), but differs in the reduced and unpigmented eye, the lack of a cleft in the inferior antennal sinus, the short segment 3 of the mandibular palp, the elongate and medially setose coxae, the broadly subcircular segment 2 of pereopods 5-7, and the acutely produced corner of epimeron 2. It differs from *Paramoerella* Ruffo, 1974, in the short segment 3 of the mandibular palp, the elongate and medially setose coxae, the broadly subcircular segment 2 of pereopods 5-7, and the acutely produced corner of epimeron 2. *Moanamoera* also differs from *Relictomoera* Barnard & Karaman, 1982, in the mammilliform (non-sinusoid) anterior margin of the head; from *Sternomoera* Barnard and Karaman, 1982, in the absence of sternal gills; and from *Pseudomoera* Schellenberg, 1929, in the more typical (non-geniculate) segment 5 of the gnathopods. *Moanamoera* is similar to *Humilomoera*, n. s-g., in the uncleft inferior antennal sinus, and in the reduced, unpigmented eye, but differs from it in the greater setosity of maxillae 1 and 2, the longer and medially setose coxae, the absence of spines from coxa 6, the acutely produced corner of epimeron 2, and the plumose third uropod. *Moanamoera* differs from *Rhithromoera*, n. s-g., in the nearly equal antennae, the setae of the gland cone, the shorter segment 3 of the mandibular palp, the slender gnathopods (with elongate segment 5 in gnathopod 2 of female), the broadly subcircular segment 2 of pereopods 5-7, the more acutely produced epimeron 2, and the plumose rami of uropod 3.

Species. *Paramoera* (*M.*) *rua* J. L. Barnard, 1977; *P. (M.) paakai* J. L. Barnard, 1977; *P. (M.) lokowai* J. L. Barnard, 1977; from the Hawaiian Islands; in brackish ponds, cave pools, and groundwater.

Etymology. From the Hawaiian word *moana* (= deep blue sea), denoting isolation in the open ocean, and *moera*, implying alliance to related genera with the same root.

Paramoera (Moanamoera) rua J. L. Barnard, 1977

Paramoera rua J. L. Barnard, 1977: 275-282, figs. 7, 8, 9 (part).

Material examined.

Hawaii: Waianapanapa Cave, Hana, Maui Island (20°45'N, 156°00'W), 24 January 1973, collected by ELB and FGH from a brackish cave pool (4 specimens).

Diagnosis. Eye poorly developed and unpigmented;

antennal sinus shallow, without a cleft; antenna 1 only slightly longer than antenna 2; major peduncular segments of antennae with about 3 groups of short setae along the ventral margins; gland cone with 2-3 moderate setae.

Inner plate of maxilla 1 with 8-10 plumose setae; inner plate of maxilla 2 with 5 plumose setae.

Segment 6 of gnathopod 1 with about 4 posterior groups of comb setae, palm with 2 outer and 2 inner barb spines; segment 6 of gnathopod 2 with 5 posterior groups of comb setae and with sparse medial setae; gnathopod 2 of female with segment 5 about 25% longer than segment 6; gnathopod 2 of male with segment 5 nearly as long as segment 6, palm oblique, palm about 50% as long as the posterior margin.

Posterior margin of segment 6 of pereopod 4 with 5 ornamental groups, each consisting of a single barb spine and a seta on its lateral side (distal spines accompanied by additional setae); posterior margin of segment 2 of pereopod 7 with shallow notches, segment 4 about 25% as wide as segment 2, longest spines of segment 5 about 60% as long as the dactyl, longest spines of segment 6 about 60% as long as the dactyl.

Posteroventral corner of epimeron 2 acute but poorly produced; posterior margin of epimeron 3 with 2-3 shallow notches, posteroventral corner angular but without a significant tooth; peduncle of uropod 1 with 7 dorsolateral spines; uropod 2 with shortened outer ramus; uropod 3 with plumose setae; telson fused about 10% its length, each apex notched, with 3-4 long setae.

Coxal gills on pereopods 2-6 (lacking on pereopod 7).

Examination of the material. Little can be added to J. L. Barnard's (1977) well illustrated description of this species. The specimens examined in the present study lacked a gill on pereopod 7 in both sexes. The oostegites are of the narrow form (cf. "*Paramoera*"). A 4.5 mm male possessed a single posterior calceolus on alternate segments 5-15 and a single medial calceolus on alternate segments 6-12 (absent from the peduncle) of antenna 1; antenna 2 lacking both calceoli and aesthetascs. Pleopod 2 is gonopodous in the male.

Size range. Both sexes to about 5 mm.

Color in life. Unknown.

Distribution. Known only from the type locality on Maui, Hawaiian Islands.

Ecology. *Paramoera (M.) rua* is found in a brackish cave pool under low light conditions. Its biology is unknown, but the absence of filtering setae on the antennae suggests that this species is primarily a detritivore, using the ventral and medial setae of the gnathopods to gather and process detrital/bacterial deposits. A single female in this collection was brooding six eggs, indicating a low fecundity. The salinity at the collecting site ranged from 2 to 4 ppt.

Remarks. The three Hawaiian species described by J. L. Barnard (1977) share many derived characters (see diagnosis of *Moanamoera*, n. s-g.). They form a closely related group,

termed a "geminate triad" by Barnard, which clearly evolved from a common ancestor. In the subsequent analyses and discussion I have lumped these three species as *Paramoera* (*Moanamoera*) spp.

Paramoera (*M.*) *rua* differs from *P. (M.) lokowai* J. L. Barnard, 1977, by the presence of eyes, by the shorter peraeopods, and by the shorter rami of uropod 3; it differs from *P. (M.) paakai* J. L. Barnard, 1977, by the setae (not spines) of the epimera, by the reduced fusion of the telson, and by the deep apical notches of the telson.

The material examined differs slightly from the original description of *P. (M.) rua*, and was termed "variant" by Barnard (1977, p. 279). These specimens possess reduced eyes and atypical ornamentation of the antennna and mandible. I have not examined sufficient material of both forms to confirm Barnard's suggestion that this constitutes a new species.

Paramoera (*Humilomoera*), new subgenus

Type species. *Paramoera* (*Humilomoera*) *leucophthalma*, new species.

Diagnosis. Rostrum unproduced; lateral cephalic lobe mammilliform; inferior antennal sinus shallow and without a cleft. Eye reduced, round, with or without pigment. Antennae of moderate length, antenna 1 longer than antenna 2; peduncular segments of antenna 1 progressively shorter, segment 1 shorter than the head; accessory flagellum 1-segmented, scale-like; ventromedial setae of peduncles short; gland cone with a single short seta; calceoli present only in male.

Upper lip entire and rubrounded; epistome unproduced. Molar triturative, oval; palp segment 2 equal to or slightly longer than segment 3; lower lip without distinct inner lobes. Maxilla 1: inner plate with 3-4 plumose setae, outer plate with 10-11 pectinate spines; palp long, segment 1 short. Maxilla 2: inner plate with a submarginal row of 2 plumose setae. Maxilliped: inner plate about as long as outer, outer plate with less than 4 medial spine teeth; palp of 4 segments, segment 1 not laterally extended, segment 3 unlobed, segment 4 shorter than segment 3, segment 4 not spinose (but with small distal setae) along the inferior margin, ungiform, with nail.

Coxae 1-3 ordinary (neither anteriorly nor ventrally produced), sparsely setose, the posterior seta slightly enlarged; coxa 4 with posterior lobe, excavate; anterior lobe of coxa 6 small to moderate in size, ventral margin of coxa 6 with spines. Gnathopods feeble, not eusirid, with subchelate oblique palm; segment 5 of gnathopod 2 subequal to or longer than segment 6 in female; gnathopod 2 of male not enlarged, palm with less than 4 barb spines in the outer row.

Dactyls of peraeopods 3-7 non-castellate, with 2 small setae near the uncinus; segment 2 of peraeopods 3 and 4 not anteriorly lobate; peraeopod 5 about 80% as long as peraeopod 7; segment 2 of peraeopods 5-7 expanded and ovate, posteroventrally lobate; segment 5 of peraeopods 5-7 shorter

than segment 6.

Pleopods ordinary; pleopod 2 of male gonopodous. Posteroventral corner of epimeron 2 not acutely produced; epimeron 3 with 2 posterior notches, the posteroventral corner with a small recurved tooth. Peduncles of uropods 1 and 2 not dorsally broadened; rami of uropod 1 subequal; outer ramus of uropod 2 shorter than inner ramus. Uropod 3 extending beyond uropod 1 (hardly so in *P. (H.) crassicauda*); peduncle without large process; rami equal in length, narrow, lanceolate, without plumose setae, but with a single simple seta on the outer margin of the outer ramus. Lobes of telson variously fused (more than half the length in *P. (H.) crassicauda*), each apex rounded, with 2 apical setae.

Coxal gills present on peraeopods 2-6 in both sexes, anterior gills reduced in female. Sternal gills absent. Female with large oostegites on peraeopods 2-4 and a smaller strap-like oostegite on peraeopod 5; oostegite of peraeopod 2 proximally broadened and wider than this coxa.

Relationships. Subgenus *Humilomoera* is like the grade "*Paramoera*" (defined above), but differs in the smaller (occasionally unpigmented) eye, the lack of a cleft in the inferior antennal sinus, the reduced ornamentation of the gland cone, the reduced setosity of maxillae 1 and 2, the less setose antennae, and the reduced gills. The broad oostegites, the spines of coxae 6, and the non-plumose uropod 3 also distinguish this subgenus from most members of "*Paramoera*." *Humilomoera* resembles *Paramoerella* Ruffo, 1974, in the reduced eye, the uncleft inferior antennal sinus, the reduced gills (small, and absent from peraeopod 7), and the non-plumose uropod 3, but differs from that genus by the structure of the accessory flagellum, the reduced setosity of maxillae 1 and 2, the absence of the inner lobes of the lower lip, and the reduced ornamentation of the telson. It differs from *Relictomoera* Barnard & Karaman, 1982, by the mammilliform (non-sinusoid) anterior margin of the head; from *Sternomoera* Barnard & Karaman, 1982, by the absence of sternal gills; and from *Pseudomoera* Schellenberg, 1929, by the more typical (non-geniculate) segment 5 of the gnathopods. *Humilomoera* is similar to *Rhithromoera*, n. s-g., in the small eye, the uncleft inferior antennal sinus, the reduced setosity of the antennae and maxillae, and the non-plumose uropod 3, but differs in the shallow depth of the inferior antennal sinus, the more feeble gnathopods, the reduced gills, the ventral spines of coxa 6, the shorter segment 5 of peraeopods 5-7, the reduced serration of epimeron 3, and the less setose telson. It is similar to *Moanamoera*, n. s-g., in the uncleft inferior antennal sinus and the reduced (occasionally unpigmented) eye, but differs in the reduced setosity of maxillae 1 and 2, the shorter coxae, the ventral spines of coxa 6, the unproduced corner of epimeron 2, and the non-plumose uropod 3.

Species. *Paramoera* (*H.*) *leucophthalma*, n. sp.; *P. (H.) crassicauda*, n. sp.; eastern North Pacific, from Alaska to Washington; in gravel and cobble substratum, ranging from marine subtidal to freshwater streambeds.

Etymology. Latin: *humilo* = humble, suggesting a reduction of many characters, and *moera*, implying alliance to related genera with the same root.

***Paramoera (Humilomoera) leucophthalma*, new species**
(Figs. 7A, 7B)

Paramoera leucophthalma Staude, 1986: 117-131, figs. 1.13 and 1.14.

"*Paramoera leucophthalma* Staude (in press)" of Staude 1987: 376 and 378.

Material examined.

Barkley Sound, British Columbia, off north shore of Cape Beale (48°48.0'N, 125°12.0'W), NMC Station B20, 5 July 1976, collected by ELB and FR aboard R/V LEIK, dredged at 30 m, in gravel and among small stones.

Holotype: female, NMC-IZ1986-055; allotype, male, NMC-IZ1986-055; 23 paratypes NMC-1976-157.

Additional material.

BRITISH COLUMBIA: Barkley Sound, British Columbia, off north shore of Cape Beale (48°48.2'N, 125°11.3'W), NMC Station B21, 5 July 1976, collected by ELB and FR aboard R/V LEIK, dredged at 20-22 m, in gravel (1 specimen); off Bordelais Islet (48°48.5'N, 125°14.0'W), 5 July 1976, collected by ELB and FR aboard R/V LEIK, dredged at 42 m in gravelly sand (1 specimen).

Diagnosis. Eye small and unpigmented; inferior antennal sinus shallow, without a cleft; antenna 1 about 40% longer than antenna 2; segment 1 of antenna 1 with a single distoventral spine; major peduncular segments of antennae with about 3 sparse groups of short setae along the posterior margins; gland cone with a single small seta.

Mandibular palp with an unusually large plumose seta at the distal end of segment 2; inner plate of maxilla 1 with 4 plumose setae; inner plate of maxilla 2 with 2 plumose setae near the inner margin.

Segment 6 of gnathopod 1 with 3-4 posterior groups of comb setae; segment 6 of gnathopod 2 with 5-7 posterior groups of comb setae and with sparse medial setae; gnathopod 2 of female with segment 5 about 10% longer than segment 6; gnathopod 2 of male with segment 5 about 75% as long as segment 6, palm oblique and about 50% as long as the posterior margin.

Posterior margin of segment 6 of pereopod 4 with 2-3 ornamental groups, each consisting of a single barb spine and a curved seta on its lateral side (the distalmost spine accompanied by long setae); posterior margin of segment 2 of pereopod 7 moderately serrated, segment 4 about 35% as wide as segment 2, spines of segments 5 and 6 not longer than 60% of the length of the dactyl.

Posterior margin of epimeron 3 with 2 distinct notches, the notch at the posteroventral corner bounded by a small tooth; uropod 3 without plumose setae; each apex of telson

with a very slender spine and a plumose seta.

Coxal gills of pereopods 2-4 reduced in female; both sexes lacking a gill on pereopod 7.

Size range. Not exceeding 4 mm.

Color in life. Unknown.

Distribution. Known only from Barkley Sound, British Columbia (latitude 49°).

Ecology. *Paramoera (H.) leucophthalma* is found interstitially in subtidal gravel, occurring deeper than any other related (*Paramoera* and allied genera) species of this region. The absence of filtering setae on the antennae suggests that this species is primarily a detrital deposit feeder. Its fecundity (2-3 eggs per brood) is notably low. Temperature at the collecting localities was about 8.0°C, and the salinity exceeded 33 ppt.

Remarks. *Paramoera (Humilomoera) leucophthalma* resembles *P. (H.) crassicauda*, n. sp., in the many character states of reduction, typical of the subgenus. It may be distinguished from that species by the unpigmented eye, the distal spine of segment 1 of antenna 1, the uniform setae of segment 3 of the mandibular palp, the more setose gnathopods, the longer carpus of gnathopod 2 of the female, the narrower bases of the posterior pereopods, the more spinose ventral margins of the epimera, the smaller peduncular spines of the uropods, the shorter outer ramus of uropod 2, the longer rami of uropod 3, and the deeper cleft of the telson. The unpigmented eye, the shallow and uncleft inferior antennal sinus, the slightly shortened segment 3 of the mandibular palp, and the elongate female carpus of gnathopod 2 are similar to the characters of the Hawaiian subgenus *Moanamoea*. The gland cone, the elongate carpus of the female gnathopod 2, the third epimeron, and the telson bear resemblance to *P. bousfieldi*, n. sp. The distinctly serrate basal segments of pereopods 5-7 and the sculpture of epimeron 3 are similar to those of *P. serrata*, n. sp.

Etymology. This species name (Gr. *leukos* white + *ophthalmos* eye) refers to the unpigmented nature of the eye. This name was proposed by Dr. E. L. Bousfield (unpublished) who used it as a provisional name in some NMC records.

***Paramoera (Humilomoera) crassicauda*, new species**
(Figs. 8A, 8B)

Paramoera crassicauda Staude, 1986: 132-142, figs. 1.13 and 1.15.

Material examined.

Steamer Bay, Etolin Island, Alaska (56°8.0'N, 132°40.0'W), summer 1981, collected by M.M. from cobble sediment in the tidal reach of Porcupine Creek.

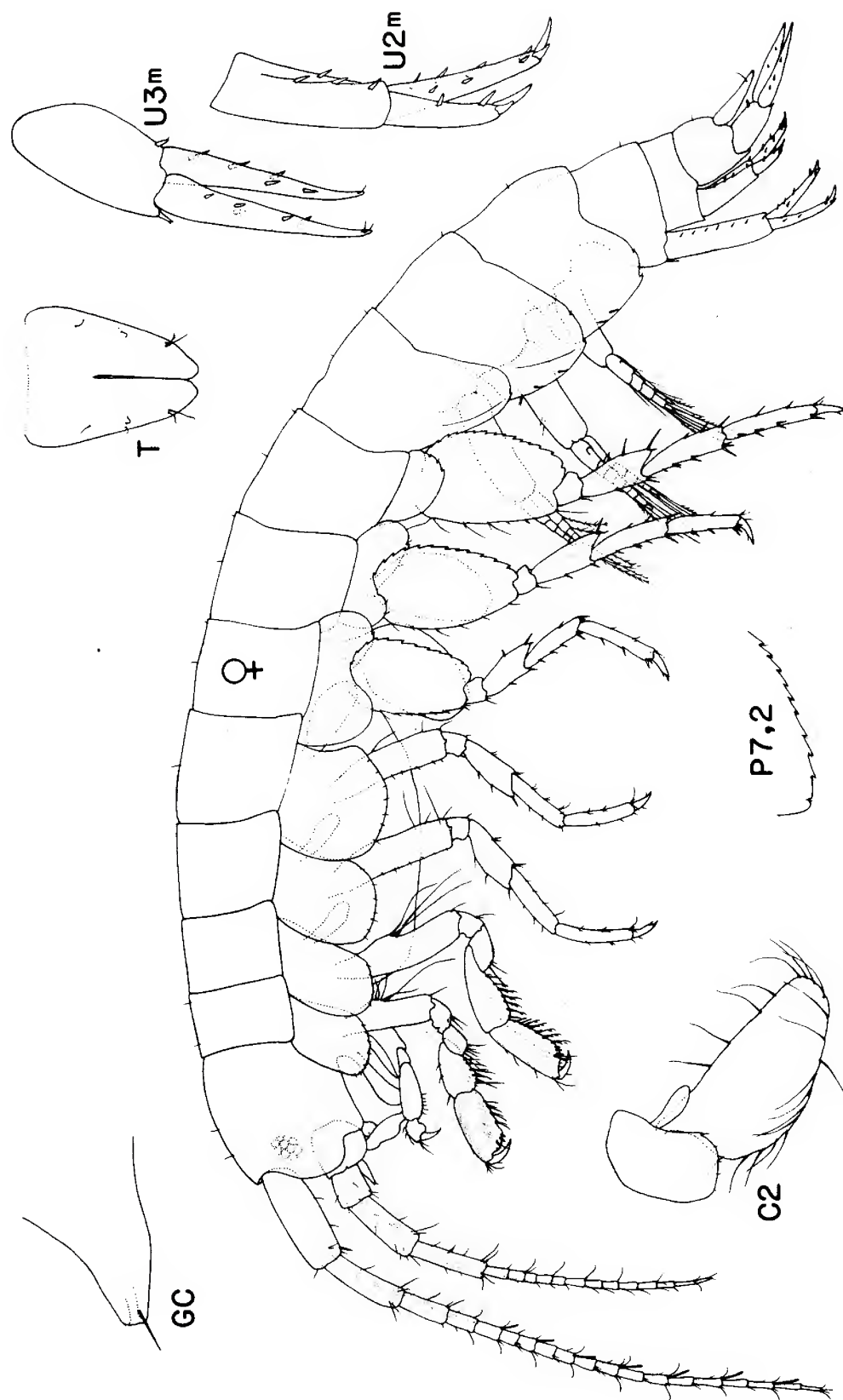


FIG. 7A. *Paramoera (Humilomoera) leucophthalma*, n. sp.; holotype female (3.6 mm); m = allotype male (3.0 mm); Barkley Sound, British Columbia.

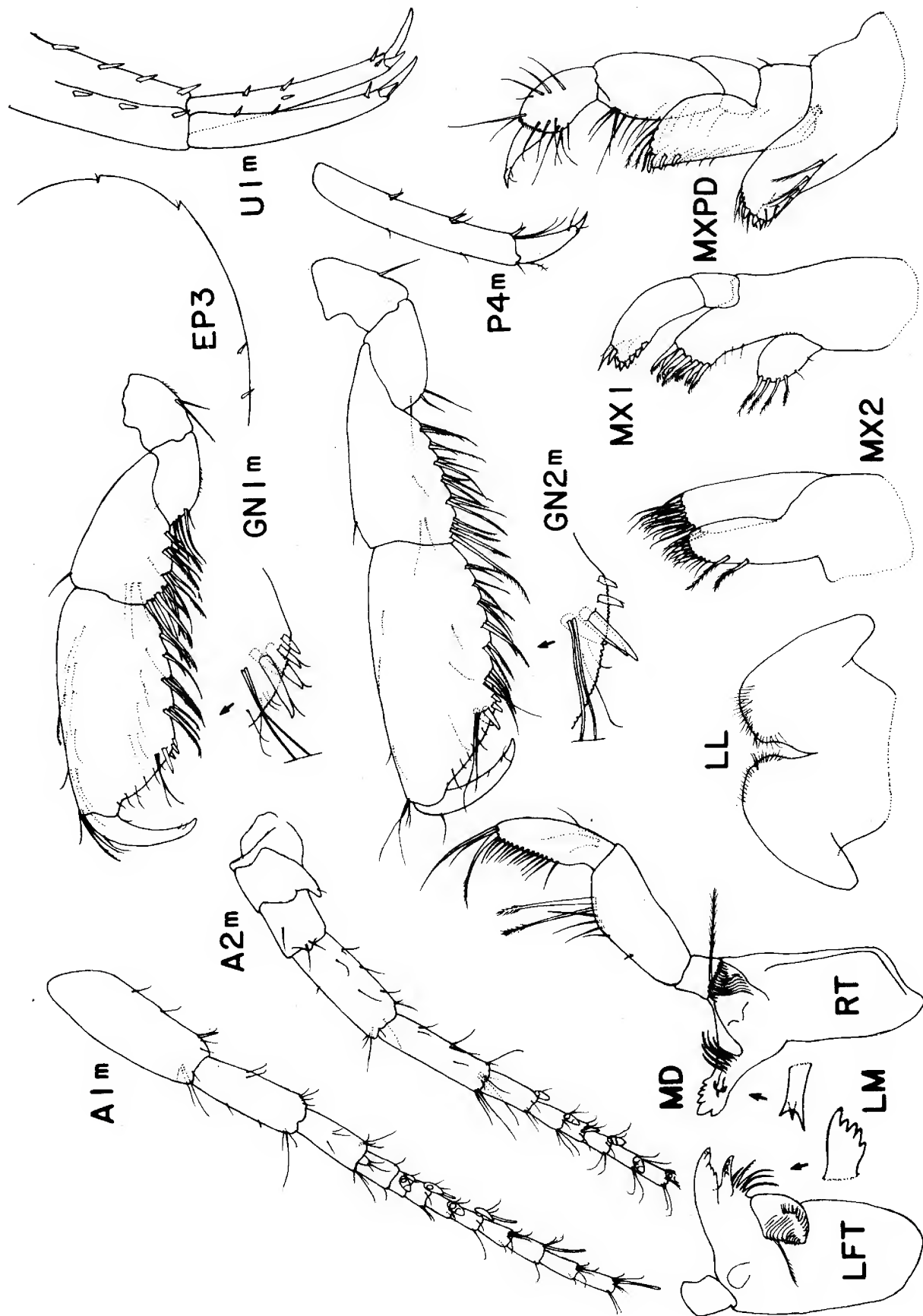


FIG. 7B. *Paramoera* (*Humilomoera*) *leucophthalma*, n. sp.; holotype female (3.6 mm); m = allotype male (3.0 mm); Barkley Sound, British Columbia.

Holotype. female, USNM-231322 (1 specimen).

Diagnosis. Eye small, pigmented; antennal sinus without cleft; antenna 1 longer than antenna 2; major peduncular segments of antennae with 2-3 sparse groups of short setae along the ventral margins; gland cone with a single small seta.

Mandibular palp with enlarged pectinate setae at the distal end of segment 2; inner plate of maxilla 1 with 3 plumose setae; inner plate of maxilla 2 with 2 plumose setae near the inner margin.

Segment 6 of gnathopod 1 with 2 posterior groups of comb setae; segment 6 of gnathopod 2 with 3 posterior groups of comb setae and with sparse medial setae; gnathopod 2 of female with segment 5 about 90% as long as segment 6, palm oblique and about 50% as long as the posterior margin; posterior margin of segment 6 of pereopod 4 with 3 spines, the central spine with a curved seta on its lateral side and the distalmost spine with 2 long setae.

Posterior margin of segment 2 of pereopod 7 moderately serrated, segment 4 about 32% as wide as segment 2, spines of segments 5 and 6 not longer than 60% of the length of the dactyl.

Posterior margin of epimeron 3 with 2 distinct notches, the notch at the posteroventral corner bounded by a small tooth; rami of uropod 3 about as long as peduncle, uropod 3 without plumose setae; telson with lobes fused about 70% of its length; each apex of telson with a stout seta and a small plumose seta.

Coxal gills reduced; female lacking a gill on pereopod 7. (male unknown)

Size range. Not exceeding 4 mm.

Color in life. Unknown.

Distribution. Known only from Steamer Bay, Alaska (latitude 58°N).

Ecology. *Paramoera* (*Humilomoera*) *crassicauda* occurs among cobbles and gravel in the tidal reach of streams. The absence of filtering setae on the antennae suggests that this species is primarily a detrital deposit feeder. Water temperature at the collecting locality reached a summer maximum of 20°C; the salinity ranged from 1 to 28 ppt (Murphy, 1984).

Remarks. *Paramoera* (*Humilomoera*) *crassicauda* shares with *P. (H.) leucophthalma* n.sp. the distinctive reduced characters of this subgenus (see remarks under *Humilomoera*). Yet it differs from that species by the pigmentation of the eye, the lack of a distal spine on segment 1 of antenna 1, the more irregular setae of mandibular palp segment 3, the less setose gnathopods, the shorter carpus of gnathopod 2, the distally broader bases of the posterior pereopods, the less spinose epimera, the larger spines of the peduncles of uropods 1 and 2, the enlarged subapical spine of the inner ramus of uropod 1, the longer outer ramus of uropod 2, the shortened rami of uropod 3, the fused nature of the telson, and the smaller gills

of pereopods 5 and 6. The reduced anterior gills of both species are perhaps a concession to increased brood space in these small-bodied species. The short rami of uropod 3 of *P. (H.) leucophthalma* are unique among North Pacific *Paramoera*, but resemble those of *P. hurleyi* Thurston 1972. Similarly the fused telson is unknown in northern species, but is like that of the Antarctic *P. walkeri* (Stebbing, 1906).

Etymology. This species name refers to the unique condition of the telson in which the lobes are fused for more than half their length. It is derived from the Latin *crassus*, meaning "that which has grown or increased" (solid or thick), and *cauda*, meaning tail.

Rhithromoera, new subgenus

Type species. *Paramoera carlottensis* Bousfield, 1958.

Diagnosis. Rostrum unproduced; lateral cephalic lobe mammilliform; inferior antennal sinus deep and angular but without a cleft. Eye reduced, round or oval, pigmented.

Antennae elongate, antenna 1 much longer than antenna 2, peduncular segments of antenna 1 progressively shorter, segment 1 shorter than the head; ventromedial setae of peduncles short and thickened; accessory flagellum 1-segmented, scale-like; gland cone with a ventrally deflexed spine; calceoli present only in male.

Upper lip entire and subrounded; epistome unproduced. Molar triturative, tall, and narrow [similar to Ueno's (1971a) figure of *Relictomoera relictata*]; palp segments 2 and 3 of subequal length; lower lip without distinct inner lobes.

Maxilla 1: inner plate with 4-5 plumose setae, outer plate with 10-11 pectinate spines; palp long, segment 1 short. Maxilla 2: inner plate not broader nor longer than outer plate, inner plate with a submarginal row of 3 plumose setae. Maxilliped: inner plate about as long as outer, outer plate with 3 or more medial spine teeth; palp of 4 segments, segment 1 laterally extended (its lateral margin nearly as long as that of segment 2), segment 3 unlobed, segment 4 shorter than segment 3, segment 4 not spinose (but with small distal setae) along the inferior margin, unguiform, with nail.

Coxae 1-3 ordinary (neither anteriorly nor ventrally produced), sparsely setose; coxa 1 with a small spine at the posteroventral corner; coxa 4 with posterior lobe, excavate; anterior lobe of coxa 6 not produced, ventral margin without spines.

Gnathopods robust and subequal in both sexes, not eusirid, with subchelate oblique palm; segment 5 of gnathopod 2 shorter than segment 6 in female, posteriorly lobate; gnathopod 2 of male slightly swollen, palm with more than 4 barb spines in the outer row.

Dactyls of pereopods 3-7 non-castellate, with 2 small setae near the uncinus; segment 2 of pereopods 3 and 4 not anteriorly lobate; pereopod 5 less than 75% as long as pereopod 7; segment 2 of pereopods 5-7 expanded and subrectangular, posteroventrally lobate; segment 5 of

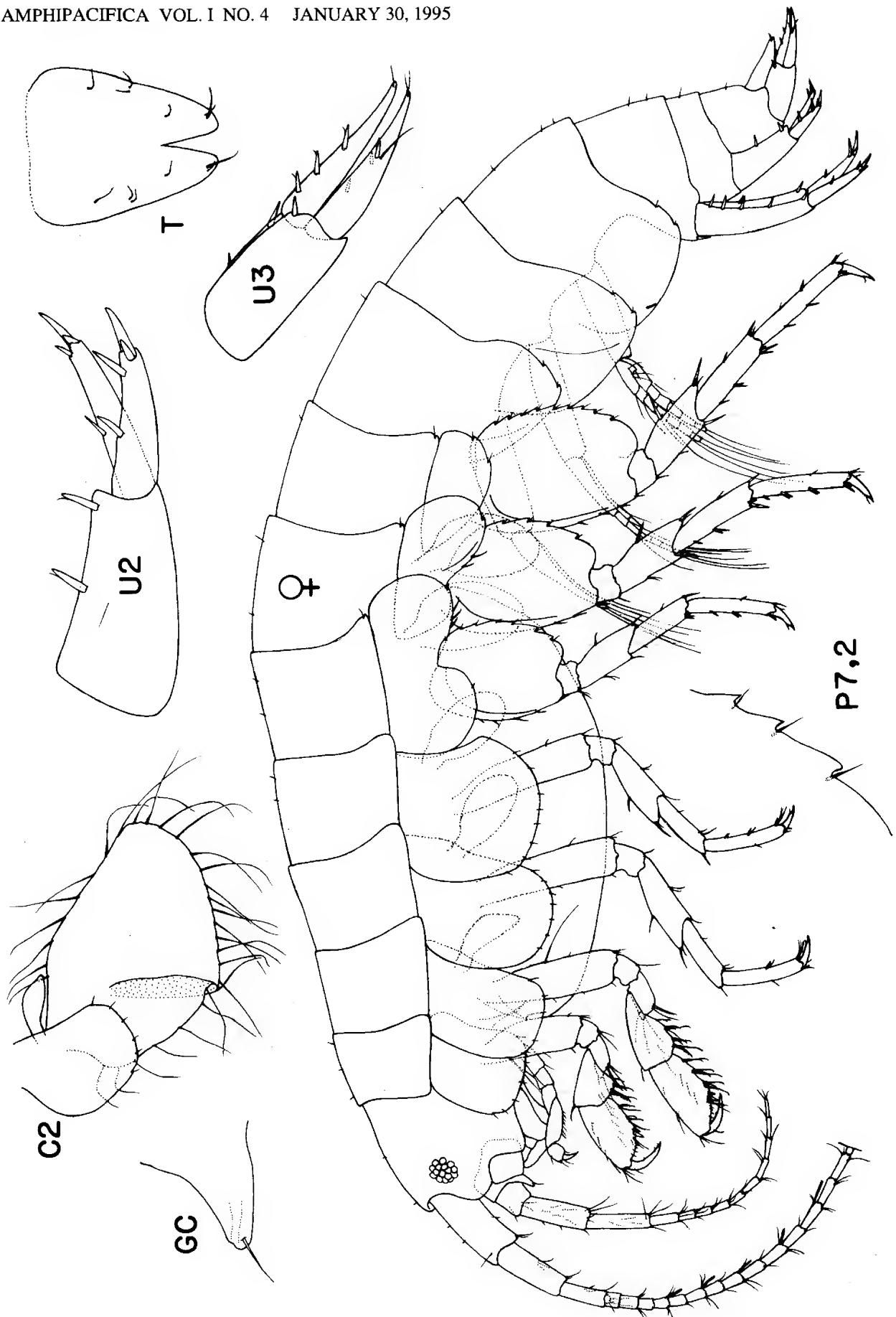


FIG. 8A. *Paramoera (Humilomoera) crassicauda*, n. sp.; holotype female (3.6 mm). Etolin Island, Alaska.

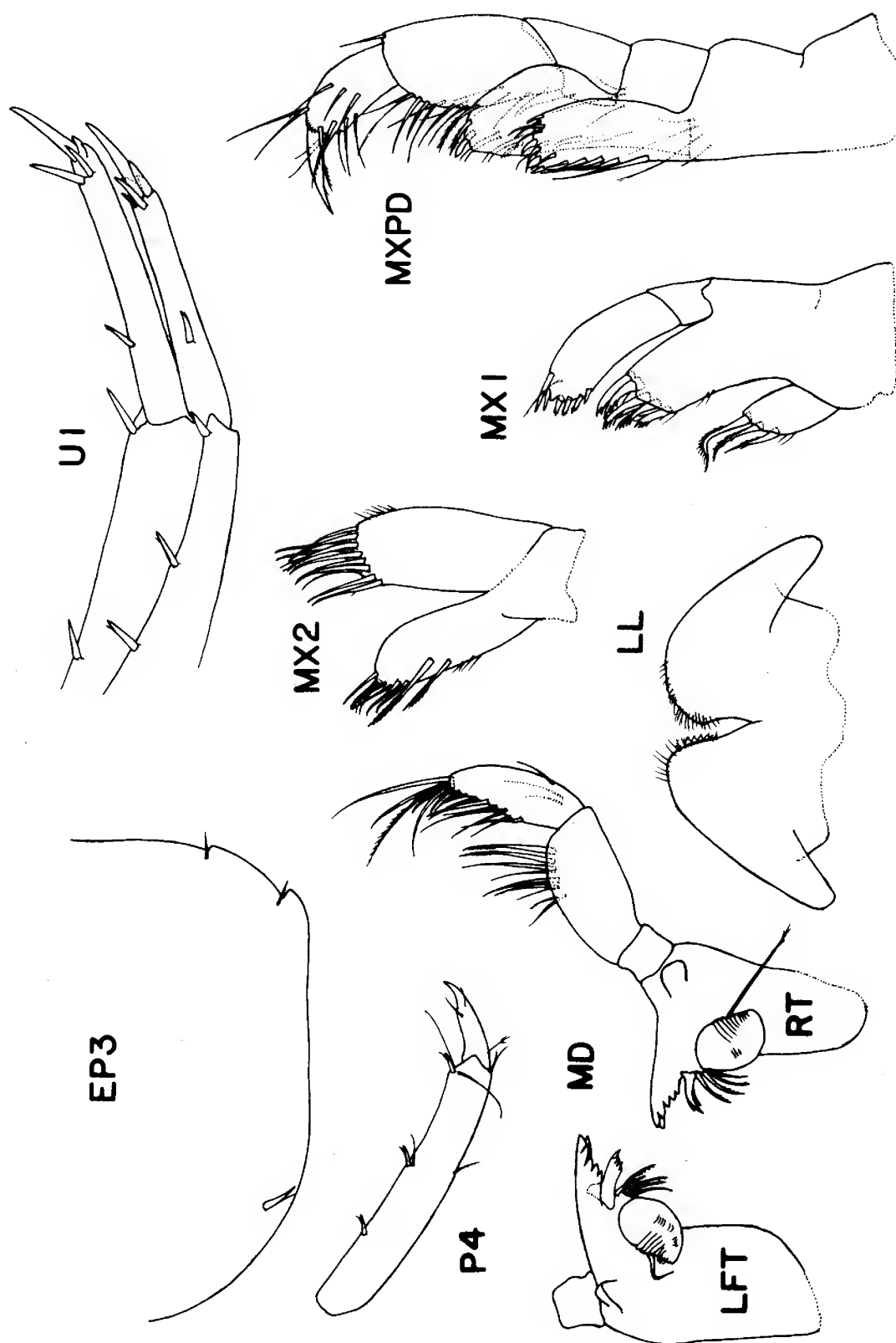


FIG. 8B. *Paramoera* (*Humilomoera*) *crassicauda*, n. sp.; holotype female (3.6 mm). Etolin Island, Alaska.

peraeopods 5-7 not shorter than segment 6. Pleopods ordinary; pleopod 2 of male gonopodous. Posteroventral corner of epimeron 2 not acutely produced; epimeron 3 with 3 or more shallow posterior notches, posteroventral corner without a distinct tooth.

Peduncles of uropods 1 and 2 with broad dorsal surface; rami of uropod 1 nearly equal; outer ramus of uropod 2 shorter than inner ramus. Uropod 3 extending beyond uropod 1; peduncle without large process; rami equal in length, narrow, lanceolate; without plumose setae but with sparse simple setae along the outer margin of the outer ramus.

Lobes of telson fused to half its length, each apex truncate, with a row of 3 or more setae.

Coxal gills present on peraeopods 2-6 and occasionally 7. Female with large oostegites on peraeopods 2-4 and a smaller strap-like oostegite on peraeopod 5; oostegite of peraeopod 2 proximally broadened, wider than this coxa. Sternal gills absent.

Relationships. *Rhithromoera* is like the grade "*Paramoera*" (defined above) but differs in the smaller eye, the lack of a cleft in the antennal sinus, the less setose antennae, the bent spine of the gland cone, the narrower molar, the reduced setosity of maxillae 1 and 2, the short peraeopod 5, the long segment 5 of peraeopods 5-7, the dorsally broadened peduncles of uropods 1 and 2, and the distinctive telson. The broad oostegites and the non-plumose uropod 3 also distinguish this subgenus from most "*Paramoera*".

Rhithromoera differs from *Relictomoera* Barnard & Karaman, 1982, by the mammilliform (non-sinuous) anterior margin of the head, the bent spine of the gland cone, the short peraeopod 5, the long segment 5 of peraeopods 5-7, the dorsally broadened peduncles of uropods 1 and 2, and the distinctive telson. It differs from *Sternomoera* Barnard & Karaman, 1982, by the bent spine of the gland cone, the reduced setae of maxillae 1 and 2, and the absence of sternal gills.

Rhithromoera differs also from *Pseudomoera* Schellenberg, 1929, by the more typical (non-geniculate) segment 5 of the gnathopods; and from *Paramoerella* Ruffo, 1974, by the reduced setae of the maxillae, and the absence of inner lobes from the lower lip. It is similar to the new subgenus *Humilomoera* by the uncleft inferior antennal sinus, the reduced setosity of the maxillae, and the non-plumose uropod 3, but differs in the deeper inferior antennal sinus, the narrower molar, the bent spine of the gland cone, the more robust gnathopods, the lack of spines on the ventral margin of coxa 6, the more serrate posterior margin of epimeron 3, the larger anterior gills, and the distinctive telson.

Rhithromoera differs from the new subgenus *Moanamoera* in the short antenna 2, the bent spine of the gland cone, the longer article 3 of the mandibular palp, the more robust gnathopods, the shorter segment 5 of gnathopod 2, the narrower segment 2 of peraeopods 5-7, the less acutely produced corner of epimeron 2, and the non-plumose uropod 3.

A deep inferior head sinus and elongate segment 5 of the hind peraeopods are characters shared by many North

American taxa within superfamily Gammaroidea (see Bousfield, 1958). However, such similarities are clearly convergent. Species of *Paramoera* and gammaroideans differ markedly in many other characters (e.g., accessory flagellum, maxillae, and uropod 3) that indicate a great phylogenetic distance between these two groups.

Species. *Paramoera* (*R.*) *carlottensis* (Bousfield, 1957); *P.* (*R.*) *bucki*, new species; eastern North Pacific, from Alaska to Washington; in pools and interstitially in gravel and cobble at the mouths of streams.

Etymology. From the Greek *rhithron*, meaning stream or riverbed, and *moera* implying alliance to related genera with the same root name.

Paramoera (*Rhithromoera*) *carlottensis* Bousfield, 1958

Paramoera carlottensis Bousfield, 195: 64-66, fig. 2; Bousfield & Hubbard, 1968: 2?; Staude, 1986: 147-151, fig. 1.16.---Staude, 1987: 376 and 378.

Material examined.

BRITISH COLUMBIA: Stiu Pt., Graham Island (53°14'N, 132°36'W), 26 July 1957, collected by ELB in brackish rock pools at stream mouth (holotype, female; allotype, male; paratypes, 1 female, 10 male/immature; NMC-2279); Gudal Bay, Graham Island (53°13'N, 132°04'W), 27 July 1957, collected by ELB at stream mouth (1 male; NMC-3744).

Diagnosis. Inferior antennal sinus deep and angular, but without a cleft; eye small to medium, dark, oval; antenna 1 about 50% longer than antenna 2; major peduncular segments of antennae with 3-4 groups of short thickened setae along the ventral margins; gland cone with a crooked apical spine and a smaller distomedial spine.

Inner plate of maxilla 1 with 5 plumose setae; inner plate of maxilla 2 with 3 plumose setae.

Segment 6 of gnathopod 1 with 4-5 posterior groups of comb setae, palm with about 6 outer and 4 inner barb spines; segment 6 of gnathopod 2 with 4-5 posterior groups of comb setae and with sparse medial setae; gnathopod 2 of female with segment 5 about 55% as long as segment 6; gnathopod 2 of male with segment 5 about 50% as long as segment 6, segment 6 widest at its midpoint, palm oblique, palm about as long as the posterior margin.

Posterior margin of segment 6 of peraeopod 4 with 4 ornamental groups, each consisting of a single barb spine and a seta on its lateral side (distal spines accompanied by additional setae); posterior margin of segment 2 of peraeopod 7 with shallow notches, segment 4 about 33% as wide as segment 2, longest spines of segment 5 about 75% as long as the dactyl, longest spines of segment 6 about 60% as long as the dactyl.

Posterior margin of epimeron 3 with 5-6 shallow notches, posteroventral notch without a significant tooth; peduncle of

uropod 1 with 7-8 lateral spines (without an isolated distoventral spine); uropod 2 with shortened outer ramus; uropod 3 without plumose setae, but with a single non-plumose seta on the outer margin of the inner ramus and a small group of non-plumose setae on the outer margin of the outer ramus; telson fused about half its length, each apex truncated, with 3-4 long setae.

Coxal gill of gnathopod 2 reduced (especially in female), both sexes with a moderately large gill on pereopod 7.

Re-examination of the type material. Bousfield (1958) described the inferior antennal sinus of these specimens as "sharply incised." Although this sinus is very angular, the inner corner is minutely rounded and is not cleft.

An obvious "median sternal process" of pereonite 2 could not be found on any of the type specimens, although the sternum of the holotype does possess a small irregular bump at the anterior margin of pereonite 1. This does not appear to be a vestigial sternal gill.

Contrary to the original description (but agreeing with Bousfield's Fig. 2), the telson of these specimens is fused for about 50% of its length.

Other material. Alaskan specimens collected by Hubbard in 1965 (Bousfield and Hubbard, 1968) and Bousfield in 1980 (NMC Stations S3B2 and S13B1; Bousfield and Jarrett, 1981) that were originally identified as *Paramoera carlottensis* should be re-examined in light of the description of *P. (R.) bucki*, new species (below).

Size range. Female to about 8 mm; male to about 7 mm.

Color in life. Unknown.

Distribution. Known with certainty from the Queen Charlotte Islands (53°N), and reported from southeastern Alaska (to 61°N).

Ecology. *Paramoera (R.) carlottensis* occurs in low salinity pools at the mouths of streams (temperature = 13°C). Its body is not as compressed as in *R. bucki*; hence it may not share the interstitial burrowing ability of that species. The setae of its antennae are not of the filtering type, but its diet is unknown. No ovigerous females have been collected. The second pleopod of the male is gnopodous.

Remarks. *Paramoera (Rhithromoera) carlottensis* may be distinguished from *P. (R.) bucki* by the larger eye, the distoventral barb spines of segment 1 of antenna 1 and segment 3 of antenna 2, the extra spine of the gland cone, the near absence of proximal setae on segment 2 of the mandibular palp, the additional seta of the inner plate of maxilla 1, and the greater number of blunt spine teeth (9-11 total) on the outer plate of the maxilliped. The gnathopods differ in several respects: *P. (R.) carlottensis* has a shorter carpus (especially in gnathopod 2), a broader propodus (its widest point is just distal to its midpoint), a greater number of posterior setal

groups (especially on gnathopod 1), and a greater number of palmar spines. *P. (R.) carlottensis* also differs by the shorter spines of the posterior pereopods, the presence of gills on pereopod 7, the more extensive serration of epimeron 3, the less spinose peduncle of uropod 1 (with shorter apical spines on the rami), the additional simple setae of uropod 3, and the greater fusion of the telson lobes. Furthermore the males of *P. (R.) carlottensis* tend to have more calceoli on the first antenna (including the peduncle).

Paramoera bucki, new species
(Figs. 9A, 9B)

Paramoera bucki Staude, 1986: 152-167, figs. 1.16 and 1.17
"*Paramoera bucki* Staude (in press)" of Staude, 1987: 376 and 378.

Material examined. Deadman Bay, Washington (48°30.7'N, 123°08.7'W), Staude station B, 23 December 1984, collected by C.P.S. in mid-intertidal beach of sandy gravel with buried cobbles in area of freshwater percolation from submergent stream.

Holotype: female, USNM-231323; allotype, male, USNM-231324; 7 paratypes, USNM-231325; 2 paratypes, NMC-IZ1986-055.

Additional material.

ALASKA: Steamer Bay, Etolin Island (56°08.0'N, 132°40.0'W), summer 1981, collected by M.M. from cobble sediment in the tidal reach of Porcupine Creek (7 specimens).

WASHINGTON: Deadman Bay, Washington (48°30.7'N, 123°08.7'W), Staude station B, mid-intertidal beach of sandy gravel with buried cobbles in area of freshwater percolation from submergent stream, April 1983 and January-November 1984 collections of CPS (>20 specimens) and 13 May 1982 collection of ELB and CPS (2 specimens), NMC 1982-251.

Diagnosis. Postantennal sinus without a notch; eye small, dark, and subcircular, antenna 1 about 50% longer than antenna 2; major peduncular segments of antennae with 3-4 groups of thickened setae along the ventral margins; gland cone with a single crooked spine.

Inner plate of maxilla 1 with 4-5 plumose setae; inner plate of maxilla 2 with 3 plumose setae; outer margin of maxillipedal palp segment 1 extending nearly to end of maxillipedal outer plate.

Segment 6 of gnathopod 1 with 3 posterior groups of comb setae, palm with 4 outer and 4 inner barb spines; segment 6 of gnathopod 2 with 5-6 posterior groups of comb setae and with sparse medial setae; gnathopod 2 of female with segment 5 about 80% as long as segment 6; gnathopod 2 of male with segment 5 about 65% as long as segment 6, palm oblique and poorly defined, palm about as long as the posterior margin.

Posterior margin of segment 6 of pereopod 4 with 4

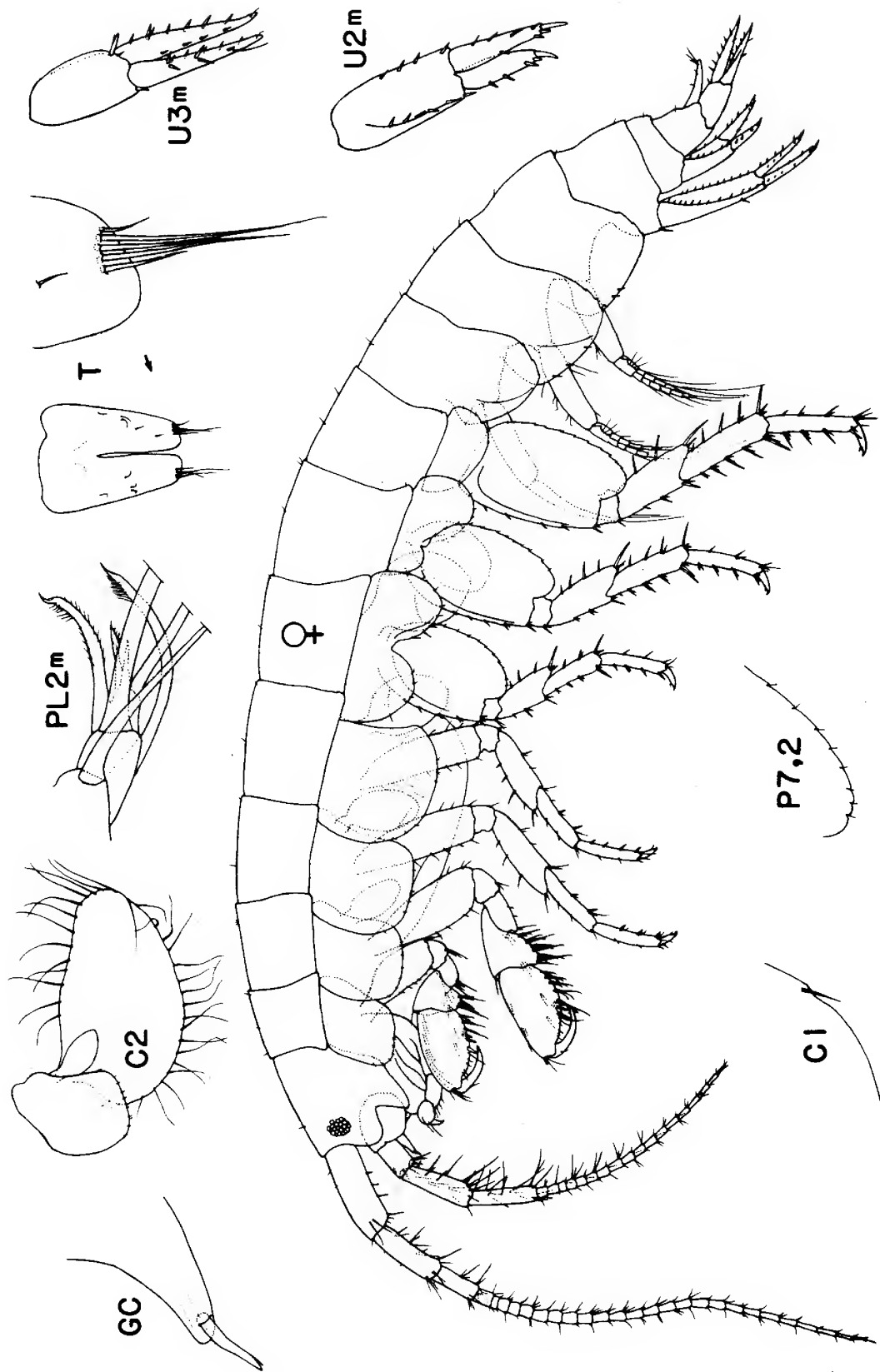


FIG. 9A. *Paramoera (R.) bucki*, n. sp.; holotype female (5.6 mm); allotype male (7.0 mm). San Juan Island, WA.

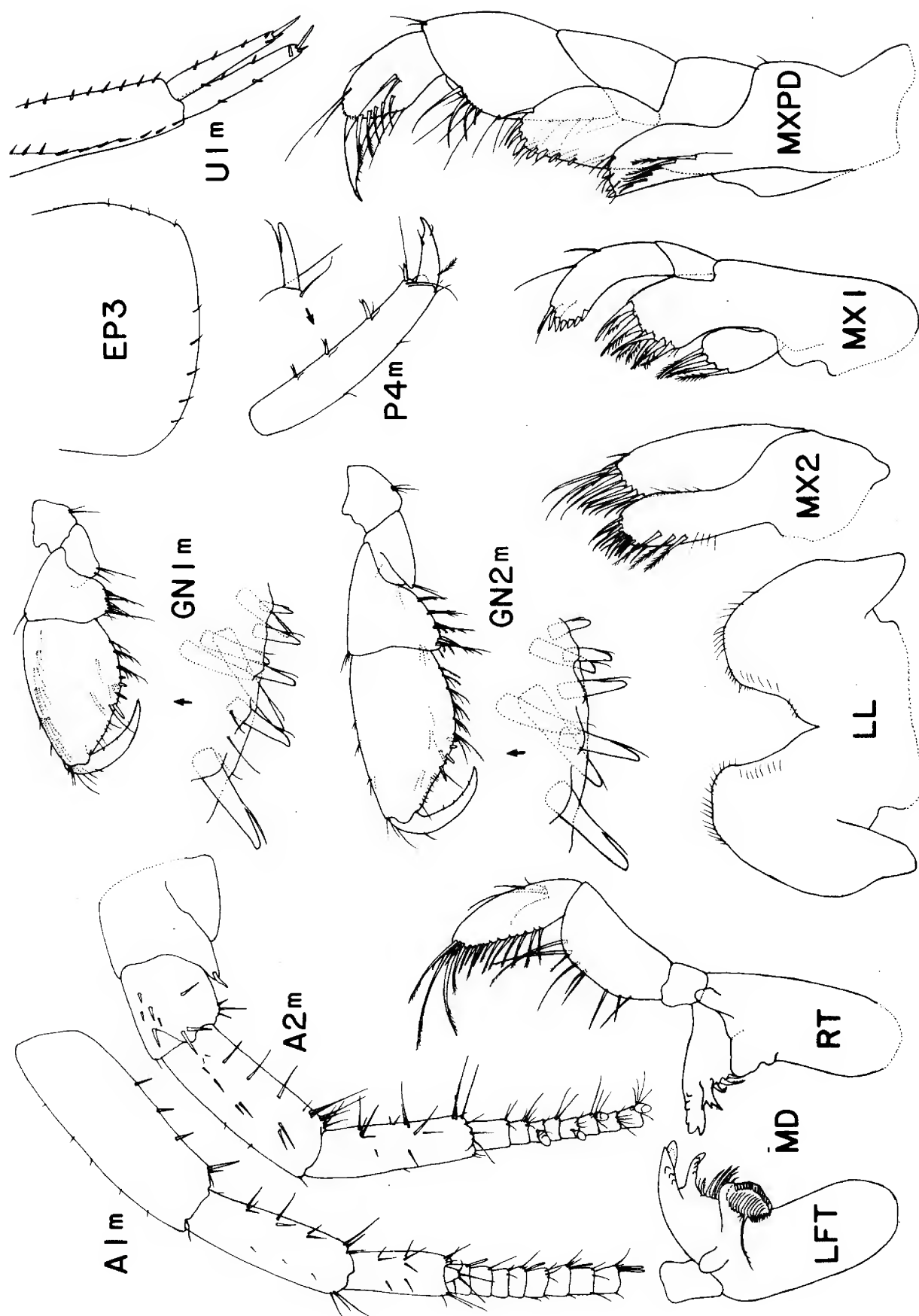


FIG. 9B. *Paramoera* (R.) *bucki*, n. sp.; holotype female (5.6 mm); allotype male (7.0 mm). San Juan Island, WA.

ornamental groups, each consisting of a single barb spine and a seta on its lateral side (distalmost spine accompanied by long setae); posterior margin of segment 2 of peraeopod 7 with shallow notches segment 4 about 40% as wide as segment 2, longest spines of segment 5 nearly as long as the dactyl, longest spines of segment 6 about 60% as long as the dactyl.

Posterior margin of epimeron 5 with 3-4 shallow notches, posteroventral notch without a significant tooth; peduncle of uropod 1 with 11-13 lateral spines and an isolated distoventral spine; outer ramus of uropod 2 shorter than inner ramus; uropod 3 without plumose setae, but with a single non-plumose seta on the outer margin of the outer ramus; each apex of telson truncated, with 3-4 long setae.

Coxal gill of gnathopod 2 reduced (especially in female); peraeopod 7 lacking coxal gill (both sexes).

Size range. Female to 6 mm; male to 7 mm.

Color in Life. Body translucent pink (without banding), eye black.

Distribution. Known incompletely from southeast Alaska (latitude 56°N) to the San Juan Islands (latitude 48°30'N).

Ecology. *Paramoera (R.) bucki* lives in the tidal reach of streambeds and in intertidal gravel beaches that have considerable freshwater seepage. Its slender body allows it to move interstitially among cobble and gravel particles. Although its antennae and gnathopods are not strongly modified for filtering, the long, stiff, flagellar setae of the second antennae are used to collect and sweep detrital food to the mouth. It could also be conjectured that the spines and stout setae of the antennal peduncles permit the entrapment and restraint of meiofaunal prey, but there is no direct evidence for this assertion. *Paramoera (R.) bucki* can tolerate rapid changes of salinity, from 0 to 32 ppt. Field measurements of salinity range from 0-28 ppt., while temperature measurements range from 8-20°C (Murphy, 1984; and pers. observ.).

Remarks. This species is very similar to *P. (R.) carlottensis* Bousfield, 1958, in sharing the derived characters of the subgenus. *Paramoerabucki* may be distinguished from *P. (R.) carlottensis*, however, by the smaller gill of gnathopod 2, its lack of a gill on peraeopod 7, the fewer blunt spine teeth along the inner margin of the outer plate of the maxilliped, the fewer setae on the third segment of the maxillipedal palp, the relatively longer carpus of the gnathopods, the larger number of spines on the peduncle of uropod 1 (especially the presence of a distoventral spine), and the presence of spines on the distal half of the rami of uropod 1. Additionally, *P. bucki* tends to lack calceoli on antenna 1 of the male, and to have fewer setae on the inner plate of maxilla 1, longer spines on segments 4-6 of peraeopods 5-7, fewer setose notches along the posterior margin of epimeron 3, and to exhibit subtle differences in the ornamentation of uropod 3.

The habitats of these two species are distinct, but may overlap near stream mouths. *Paramoera (R.) bucki* may also co-occur with *P. (H.) crassicauda*. These species are similar in having a small pigmented eye, but *P. bucki* can be distinguished by its deeper inferior antennal sinus, its more robust gnathopods, the longer rami of its third uropod, and by the deep cleft and multiple setae of the telson.

Etymology. This species is named for Mr. Sam Buck, owner of the upland property of Deadman Bay during the author's field studies, and in grateful acknowledgement of his assistance in the author's research performed at Friday Harbor Laboratories.

DISCUSSION

New descriptions.

The six new species of *Paramoera* described here tend to confirm the richness of the overall amphipod fauna of the eastern North Pacific. Bousfield (1981) estimated that this region has more gammaridean species than the western North Pacific or either eastern or western coasts of the North Atlantic. Other taxonomic investigations (e. g., Dickinson, 1982; Conlan, 1983; Jarrett and Bousfield, 1994), involving several other superfamilies, have each revealed a surprising number of previously undescribed species from this coast.

Although the majority of species of *Paramoera* have been described from the southern hemisphere, it is now apparent that this genus is well established in the eastern North Pacific. A total of nine species and one subspecies are here recognized from the west coast of North America and three from the Hawaiian Islands.

Classification.

It is beyond the scope of this work to fully define the genus *Paramoera*. New insights, however, have been gained by examining the eastern North Pacific representatives of this group. It is clear that at least four of these species bear a strong relationship to the "type" form of the sub-Antarctic. In contrast, three new subgenera have been identified that possess apomorphic characters and help to define the evolutionary trends within *Paramoera* as a whole.

The decision to erect these new groups as subgenera was carefully considered. The more common practice has been to erect a full genus for any new species or small flock of species that seem separated by a gap from all known relatives (*sensu* Mayr, 1969). Examples include the creation of the genus *Paramoerella* Ruffo, 1974, for *P. interstitialis*; the genus *Antarctogeneia*, Thurston, 1974, for *A. macrodactyla*; and the genus *Relictomoera* J.L. Barnard and Karaman, 1982, for *Paramoera relict* Ueno, 1971 (Ueno, 1971a), and *Paramoera tsushimana* Ueno, 1971 (Ueno, 1971b). This proliferation of small genera within the Pontogeneiidae has been criticized by Shaw (pers. comm.). Barnard & Karaman (1982), elsewhere prolific authors of new amphipod taxa, have

hesitated to add "yet another monotypic genus to the pool."

The subgenera proposed here might make equally valid genera, but for a few considerations. Most important are the matters of scale (cf. Stimpson, 1961) and information content (Wiley, 1981). If we continue the trend of creating a new genus for each distinctly different species or species pair, we belittle the significance of the genus. At the same time we lose information about relationships. Admittedly this is all relative to the higher classification scheme. But since we presently deal with gammarideans only in terms of species, genus, family, and superfamily, any group within *Paramoera sensu lato* that is elevated to generic status loses any obvious alliance to *Paramoera* within the Pontogeneiidae. In the case of *Paramoera*, workers have tried to retain this sense of relationship by maintaining the root "moera" in the names of most new descendant genera. Nevertheless, ingenious nomenclature should not be made to compensate for inadequate classification.

The subgenus concept has not enjoyed wide use within the superfamily Eusiroidea. Thurston (1974) and Sagar (1976) have considered the creation of a new subgenus or genus to contain *Paramoera walkeri* (Stebbing, 1906), and J. L. Barnard (1977) suggested that the Hawaiian *Paramoera* might qualify as a new subgenus, but neither has been formally erected. Subgenera were utilized within the old concept of Gammaridae, but this unwieldy group has now been reorganized into new families and full genera (Bousfield, 1977, 1979) and subsequent revisors.

One undeniable advantage of using subgenera for groups within unresolved taxa is the minimal disruption of practical taxonomy (e.g., the use of species lists in environmental surveys) where only the genus and species names are commonly used. This is especially appropriate for *Paramoera*, because further revisions are expected (Shaw, 1984; Thurston, pers. comm.).

The alternative to a subgeneric classification would be to recognize such taxa as genera, but expand the higher categories of the Eusiroidea. For example, a subfamily "Paramoerinae" might be erected to receive *Paramoera sensu stricto* and its allied genera within the family Pontogeneiidae. Such may be the eventual disposition of these new subgenera, as in the case of "good old Gammaridae." But regardless of the exact scheme, future efforts should insure the monophyletic integrity of the component groups. Ideally, the classification should reflect the true pattern of evolutionary descent.

The new subgenera *Rhithromoera* and *Humilomoera* are clearly distinguished by both phenetic and phylogenetic methods (Fig. 10). *Moanamoera* also appears strongly "dissimilar" to the base grade "*Paramoera*" in the phenogram (Fig. 10a). It would have formed a narrowly defined clade in Fig. 10b, if the three species of this subgenus were evaluated as separate taxa. Not only do these subgenera form well defined clusters or clades, but they are distinguished from members of the grade "*Paramoera*" by a dozen or more synapomorphies (enumerated by Staude, 1986). In contrast, the lower branches of the grade "*Paramoera*" are separated by only two or three derived features.

The remaining grade "*Paramoera*" is somewhat of a strawman. It is presently a taxon of convenience, a paraphyletic grade waiting to be revised by subsequent workers. Of its eastern North Pacific members, *P. bousfieldi* is the least congruent; thirteen apomorphies (Staude, 1986) distinguish it from the other members of this group. In the southern hemisphere, *P. walkeri* differs by its poorly setose maxillae, toothed dorsum, and largely fused telson, characters worthy of subgeneric distinction. Other subgenera will become evident as additional species are described and after the known southern species have been redefined.

Evolutionary trends

The fossil record of the Gammaridea is poor (Bousfield, 1982; Bousfield and Shih, 1994) and provides no useful insight into the ancestral state of *Paramoera*. We must therefore look to extant groups to understand the evolution of this genus.

The evolutionary reduction of body parts and ornamentation has been recognized within the Crustacea as a whole by a number of workers (e.g., Sanders, 1963; Bousfield, 1978; Boxshall, 1983; Hessler, 1983). In the Amphipoda the accessory flagellum has long been accepted as a primitive character (J. L. Barnard, 1969a, 1974) that has been lost in the more advanced groups. Within Pontogeneiidae, the fully setose condition of the maxillae has been considered plesiomorphic by J. L. Barnard (1972b) and Thurston (1974). Furthermore, primitive species would be expected to have well developed gills on pereopod 7 (Bousfield, 1983). These characters are present in the South African species, *Paramoera bidentata* K. H. Barnard, 1932 (see Methods and Fig. 1), which is thought to be close to the ancestral species of *Paramoera*. That is not to say that *P. bidentata* is entirely plesiomorphic; its spinose antennae and toothed pleonites are derived characters.

The presence of calceoli in both sexes of *P. bidentata* (Fig. 1) is a primitive condition at the genus level (cf. Bousfield 1985), but on a larger scale is considered to be derived (Bousfield and Shih, 1994). Calceoli are absent from the female in nearly all other species of *Paramoera* (for a possible exception see J. L. Barnard's, 1972a, Fig. 38 of *P. chevreuxi*). Bousfield (1980; 1985) has observed that calceoli are reduced in the male of some hypogean forms. Indeed, the quasi-hypogean *P. (Rhithromoera) bucki*, often lacks calceoli on antenna 1 of the male. The poorly known males of *Moanamoera* also seem to exhibit a reduction of calceoli. The fine structure of the male calceolus is consistent within the eastern North Pacific *Paramoera* (like that of the male *P. bidentata*, Fig. 1), and is in approximate agreement with the findings of Lincoln and Hurley (1981). It is, however, noteworthy that the calceolus of antenna 1 in the female of the primitive *P. bidentata* is a three-element structure like that of *Gondogeneia* (J. L. Barnard, 1972a, 1972b), while the calceolus of antenna 2 is reduced to a discoid proximal element and a straplike distal element reminiscent of *Amathillopsis australis* Stebbing (Lincoln and Hurley, 1981).

The trend in character reduction within *Paramoera* is

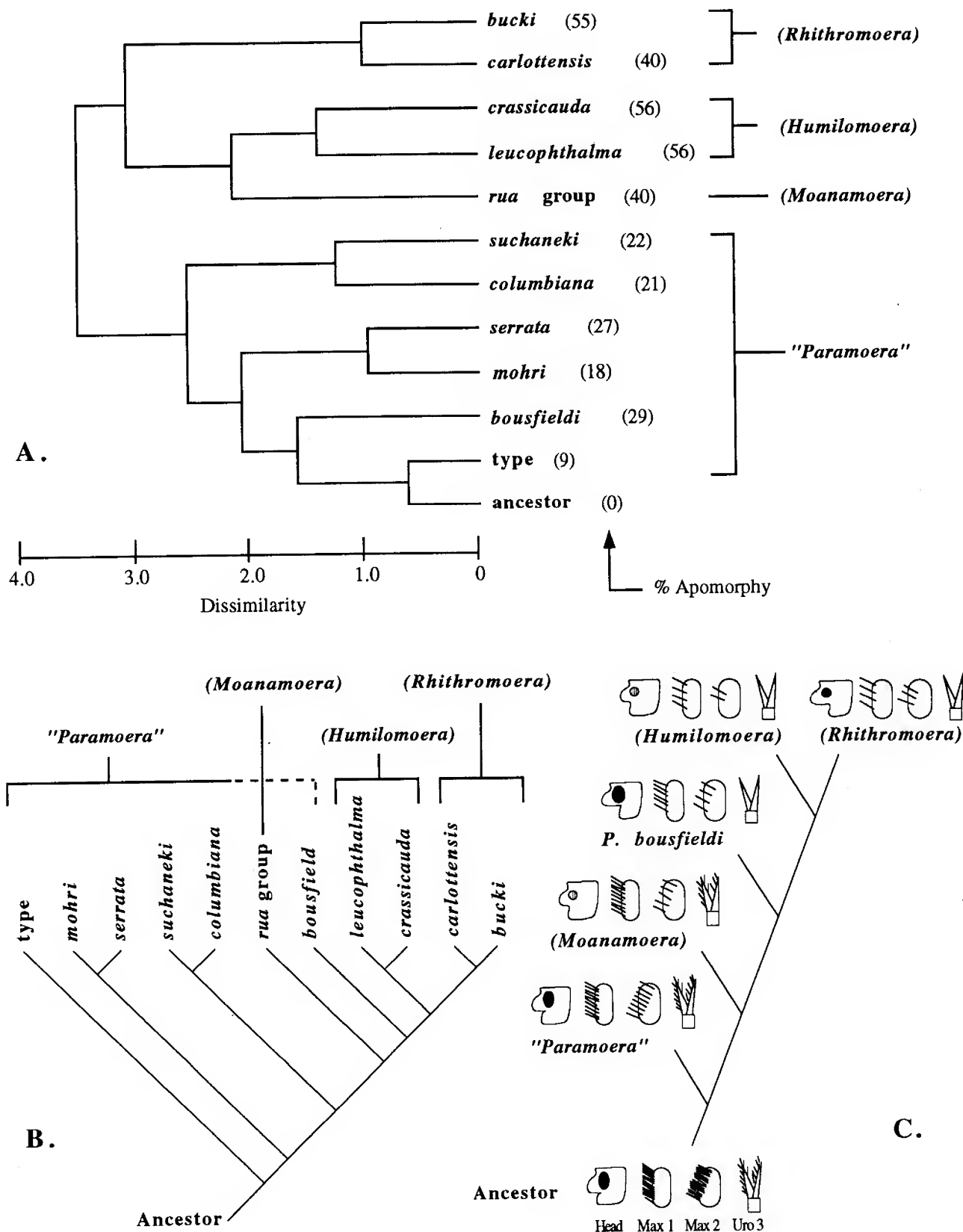


FIG. 10. Phyletic analyses of regional species of *Paramoera* compared to the type and ancestral forms based on 52 characters; A. dendrogram produced by phenetic clustering; B. cladogram generated by PHYLIP; C. phyletic diagram of selected characters, which are reduced in the apomorphic subgenera.

schematically illustrated in Fig. 10c. In the more advanced subgenera there is a decrease in eye size and a loss of setae from maxillae 1 and 2. Gills are also reduced in size and lost from pereopod 7 (illustrated by Staude 1986) in most members of these subgenera. The plumose setae are lost from the third uropod in *Humilomoera* and *Rhithromoera*, and some apomorphic species exhibit partial fusion of the telson lobes.

The ancestral *Paramoera* likely had setose antennae and a full compliment of comblike setal groups on the posterior, medial, and anteromedial surfaces of the gnathopods. Modern species of *Paramoera* utilize these setae as a filtering apparatus to collect suspended particulates from the water column and from the interstitial water within the sediment (Staude, 1986). It does not preclude them from feeding on macroalgae, detrital deposits, or even meiofauna. This feeding-type, perhaps inherited from a proto-crangonyctoid lineage (Bousfield, 1985), probably contributed to the successful radiation of this group. This may have coincided with an increase in plant-derived particulates in the Cretaceous (Bousfield, 1978; Bousfield & Shih, 1994). The more advanced subgenera have forsaken the old ways; their reduced setae are apparently sufficient to collect an adequate detrital meal in their present environments.

Concurrent with this reduction of characters has been a general tendency to enter freshwater. Nearly all members of the advanced subgenera are found in fresh or low salinity waters, while the "*Paramoera*" prefer high salinities. Exceptions include *P. (Humilomoera) leucophthalma*, which is a shallow subtidal coastal marine form, and the transitional *P. bousfieldi*, which prefers marine intertidal areas with freshwater seepage. *Paramoera columbiana*, although a member of the grade "*Paramoera*," is often found in the tidal portion of streams. This penetration into freshwater is also reported for the related Japanese genera, *Relictomoera* and *Sternomoera*, and for *Pseudomoera* in Australia (J. L. Barnard and Karaman, 1982).

Paramoera columbiana also diverges from its congeners by the non-gonopodous second pleopod of the male and the high fecundity of the female. Future investigations of *Paramoera* in other geographic regions should consider these differences in reproductive biology. Examination of the fine structure of the male pleopod 2 and the precopulatory carrying positions (described for *Paramoera mohri* and *P. bousfieldi* by Staude, 1986, and for *P. columbiana* by Bousfield and Shih, 1994) will provide added clues to the phylogeny of this group. The structure of the gills and the breadth of the oostegites, ignored in all previous descriptions within the genus, have also been shown to be of phylogenetic importance. Although the structure of the calceolus is consistent in eastern North Pacific species, the unique calceoli of the female in *P. bidentata* may help link *Paramoera* to other genera within the Pontogeneiidae.

Biogeography

An estimate of global species richness of *Paramoera* and its allies is presented in Table 3. Although the data (compiled

from many sources, especially J. L. Barnard, 1972a; Thurston, 1974; Bellan-Santini and LeDoyer, 1974; Lowry and Bullock, 1976) suffer from uncertain identifications and unresolved synonymies, some general trends can be observed.

The area of greatest species richness is the region of the Antarctic Peninsula (West Antarctica) through the Scotia Ridge to Tierra del Fuego. The eastern sub-Antarctic islands (i.e., Crozet, Kerguelen, Campbell, Auckland, and Macquarie) taken together are equally rich. Interestingly, many of these southern species are reported over wide ranges. For example, *Paramoera gregaria* (Pfeffer, 1888) has been found at Kerguelen Island (60°E), Macquarie Island (160°E), the Ross Sea (180°E), Cape Horn (65°W), South Georgia (40°W), and Tristan da Cunha (10°W). Whether this apparent low endemism is an artifact of misidentification or the result of a natural phenomenon (e.g., West Wind Drift) cannot be determined at this time.

TABLE 3. Global species richness of *Paramoera* and its closely allied genera.

Region	# spp <i>Paramoera</i> +allies
Eastern North Pacific	9/9
Western North Pacific (Japan)	4/9
Hawaiian Islands	3/3
Eastern tropical Pacific	0?/0?
Western tropical Pacific	0?/0?
Eastern South Pacific	2?/2?
Oceania	0?/0?
Australia	1?/3
New Zealand	2/3
East sub-Antarctic islands	10/10
Scotia Arc/West Antarctic	10/10
East Antarctica	2/2
South Atlantic	4/4
South Africa	1/3
Central and North Atlantic	0/0
Arctic	0?/0?

The six new species of *Paramoera* described here from the eastern North Pacific have elevated the richness of *Paramoera* in the North Pacific to a level only slightly below that of the sub-Antarctic. By considering the closely allied genera, *Relictomoera* and *Sternomoera* of Japan, it can be observed that this species richness is equally balanced on the eastern and western shores of the North Pacific.

South Africa is the home of one of the most primitive species of *Paramoera* (i.e., *P. bidentata*). It appears that most austral *Paramoera* are plesiomorphic (e.g., very setose antennae, maxillae, and gnathopods), although many are known only from sketchy original descriptions. Exceptions include *P. hurleyi* Thurston, 1972, from the South Orkneys; *P. walkeri* (Stebbing, 1906), common in the eastern Antarctic;

and *Pseudomoera gabrieli* (Sayce, 1901) from inland streams of Australia. [Interestingly, a number of other southern pontogeneiid genera (e.g., *Bovallia* Pfeffer, 1888; *Pontogeneiella* Schellenberg, 1929; *Schraderia* Pfeffer, 1888; and *Zaramilla*, Stebbing, 1888) possess fully setose maxillae, but these do not have plesiomorphic counterparts in the northern hemisphere.]

In contrast, many apomorphic groups are found in the North Pacific. The new subgenera *Humilomoera* and *Rhithromoera* display numerous advanced characters (discussed above). The Hawaiian *Moanamoera* and the Japanese *Relictomoera* and *Sternomoera* have moderately setose maxillae, but are apomorphic in many other respects (e.g., reduced eyes, less setose antennae and gnathopods, and sternal gills). Nevertheless, some plesiomorphic taxa may be found on either side of the North Pacific (e.g., *Paramoera koreana* Stephensen, 1944, from Korea and *P. suchaneki* n.sp., from the United States).

Along the west coast of North America there is no clear biogeographic trend in apomorphy. The advanced subgenera, however, are mainly recorded from British Columbia and southeast Alaska, while the relatively plesiomorphic species within the subgenera have been found south of the Strait of Juan de Fuca. This observation contrasts somewhat with the findings of Bousfield (1981), Bousfield and Hendrycks (1994), and Bousfield & Jarrett (1994) whereby the more apomorphic species of talitroidean, pleustid, and phoxocephalid amphipods respectively, tend to be found at lower latitudes along this coast.

Any palaeobiologic explanation of this distributional pattern must be argued without the benefit of fossil information, and for this reason is very speculative. By the criteria of Bousfield (1983), the *Paramoera* lineage is primitive relative to most other gammarideans. Since the origin of the Gammaridea is thought to have occurred in the late Paleozoic (J. L. Barnard & C. M. Barnard, 1982; Bousfield & Shih, 1994), it is conceivable that ancestral *Paramoera* were present in the shallow seas among the microplates of southwestern Gondwana as this supercontinent was breaking up during the Cretaceous Period, about 150-125 m.y. BP (Pielou, 1979; Martin, 1986).

The South African *Paramoera bidentata* might therefore be seen as a plesiomorphic relict, surviving as small populations in restricted intertidal areas of coarse sediment (Griffiths, pers. comm.). Barnard & Barnard (1982) have offered a parallel argument to explain the distribution of freshwater crangonyctins, suggesting that South Africa has drifted into unfavorable latitudes for cold-adapted groups and has become a "dying environment... with some relicts."

The cold waters of Tierra del Fuego and the Antarctic Peninsula might serve as a plausible center of origin from which *Paramoera* has radiated circumpolarly and northward into the Pacific. The paradigm of a "center-of-origin" dominated by plesiomorphic species has been criticized by advocates of vicariance, but Pielou (1979) concedes that some distributions (Schminke, 1974) are still best explained by this process. Indeed all vicariance hypotheses assume the

prior dispersal of the ancestral taxa (Kohn, 1983).

This line of reasoning demands some effective means of dispersal. Sagar (1980; and papers cited therein) states that juveniles of *P. walkeri* migrate offshore. My own observations of *P. mohri* and *P. serrata* (Stauder, 1986) have shown that these species make nocturnal excursions into the nearshore plankton. Hence, any arguments that *Paramoera* is an intertidal benthic brooder with poor dispersal potential might be countered. Additionally, J. L. Barnard (1970) emphasized adult rafting as a primary means of amphipod dispersal, a hypothesis supported by the observations of Highsmith (1985). This evidence might be sufficient to explain the diverse sub-Antarctic distribution, by invoking the aid of the West Wind Drift in the Cenozoic to carry amphipods (singly or attached to drift algae) around the southern continent.

The dispersal of *Paramoera* into the North Pacific is harder to explain. Barriers of warm water and unsuitable substratum would seem to block any northward passage, just as *Paramoera* has presumably been barred from the Central and North Atlantic. In jumping this gap, the brachyuran genus *Cancer* is said to have "transgressed the tropics by submergence" (Garth, 1961). *Paramoera*, however, is almost exclusively intertidal in the North Pacific, preferring coarse substrates and an algal/detritus food source; no subtidal representative has been found by intensive sampling off southern California (J. L. Barnard, 1962).

Some temperate species of *Paramoera* will survive for weeks at room temperature (pers. obs.), and the three tropical species from Hawaii provide further evidence that temperature constraints are not insurmountable. Brusca and Wallerstein (1979) concluded that temperature was less important than predation and the presence of suitable substratum in restricting the range of the cold-water isopod genus *Idotea*.

Paramoera walkeri seasonally inhabits the bottom of sea ice (Sagar, 1980), and *P. ?pfefferi* Schellenberg, 1931, occurs on the buoyant blades of the kelp *Macrocystis* (A. Escofet, pers. comm.). Attachment to drifting icebergs or dislodged kelp might have enhanced the success of long range northward dispersal of ancestral species (the former case avoiding the thermal barrier). These mechanisms may have been more likely under the climatic conditions and ocean currents of earlier geological periods.

The penetration of this group into the freshwater epigean and hypogean environments of Japan (evolving sternal gills in the case of *Sternomoera*) suggests a considerable residence time in the North Pacific. Speaking of the North Pacific rim, Bousfield (1981) wrote: "Tectonic movements and crustal upheavals in this region are extensive and frequent, and over the millenia have produced a broad spectrum of intertidal and coastal environments with nutrient rich waters in which an ancient and varied biota has developed." Here periodic outbreaks of gammaridean speciation may have occurred as recently as the Pleistocene (Golikov & Tzvetkova, 1972), spawned by the rapidly changing glacial conditions of this region. Perhaps established in the North Pacific as early as the Mesozoic, the genus *Paramoera* has been subjected to the vicariant effects of these tectonic and glacioeustatic events

for eons, producing the species that we see today.

The presence of this typically cold-water group on the tropical, mid-ocean islands of Hawaii remains anomalous. J. L. Barnard (1977) theorized that these species evolved from a marine ancestor which emigrated from North America or Asia during a cool-water Hawaiian epoch. Although *Moanamoera* does bear affinities to *Humilomoera* spp. and *Paramoera bousfieldi* of western North America, it diverges by many distinctive characters. This argues for a long isolation from all known congeners, and descent from an ancestral type which is now extinct (or undiscovered) elsewhere. The islands of Hawaii and Maui are hardly more than 1 m.y. old, while the islands to the west of the chain increase in age to nearly 70 m.y. (Rotondo et al., 1981). Hence the *Moanamoera* group may have inhabited the Hawaiian-Emperor archipelago for some time, repeatedly island hopping to the younger islands. Bousfield & Howarth (1976) proposed a similar west-to-east colonization of the cave dwelling talitrid amphipods found on Kauai. A continued search for traces of the *Moanamoera* lineage on the older islands of this chain, as well as on more distant island groups, might be very rewarding, offering a test of vicariance hypotheses (e.g., Springer, 1982).

Several authors (Rotondo et al., 1981; Springer, 1982; Kohn, 1983) have proposed that a series of older (>70 m.y.) islands moving north on the Pacific plate from a volcanic hotspot south of the equator was the source of some of the biota presently found on the Hawaiian chain. Similarly, paleontological and geomagnetic evidence (Monger & Ross, 1971; Coney et al., 1980) indicates that some of the Mesozoic terranes which now make up the coast of British Columbia and Alaska also formed at low latitudes and have moved great distances along this coast. Perhaps these too have helped to carry *Paramoera* into the North Pacific, where it survives today as a significant part of the gammaridean fauna.

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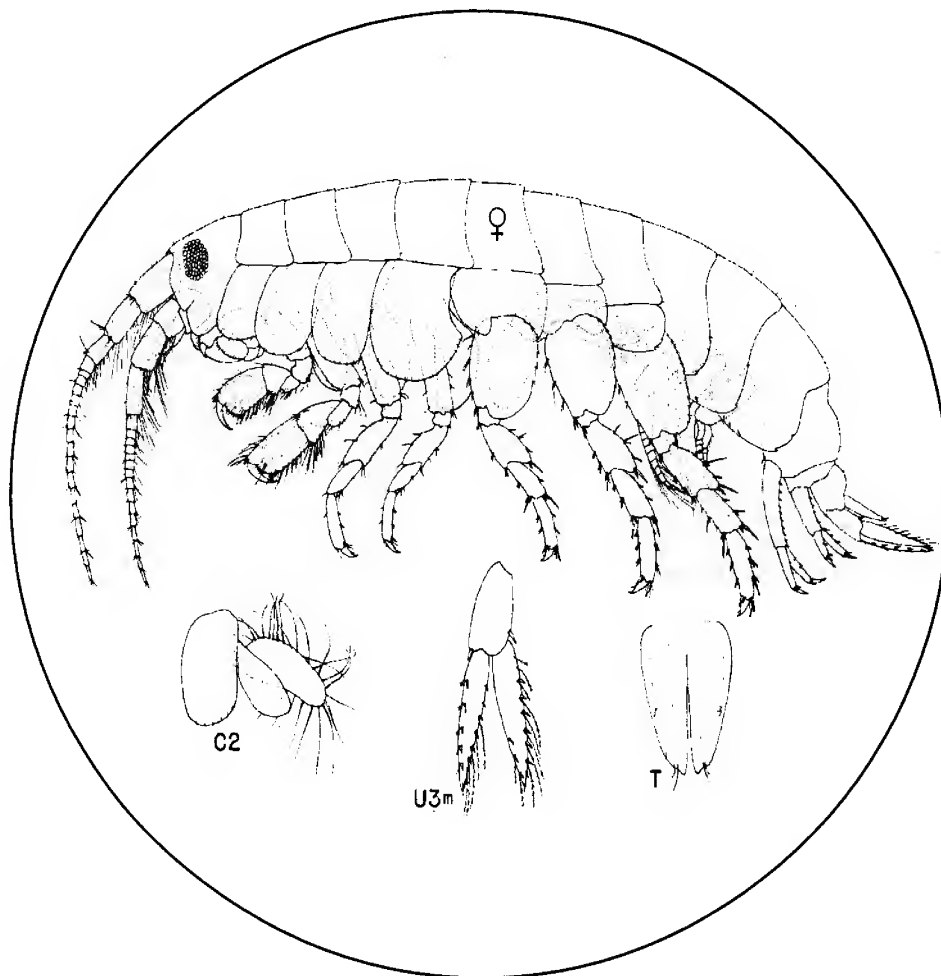
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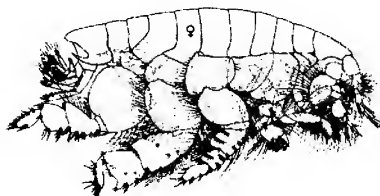
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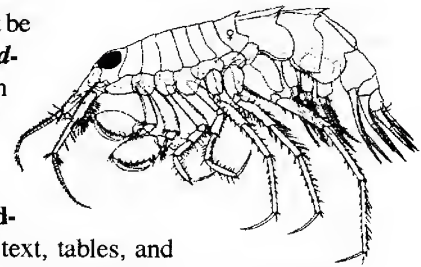
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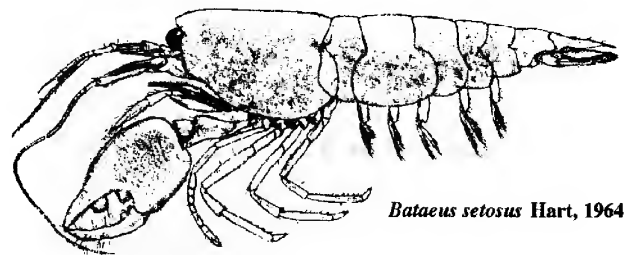
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